

The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop

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Synopsis

The type upper Caradoc rocks of south Salop are reviewed and a new lithostratigraphical and biostratigraphical scheme and revised chronostratigraphical nomenclature presented. Around the Onny Valley five formations are erected, in ascending order the Horderley Sandstone Formation, Alternata Limestone Formation, Cheney Longville Formation, Acton Scott Formation and Onny Shale Formation. The Cheney Longville Formation is divided into a lower Glynboro Member and an upper Crosspipes Member. The Acton Scott Formation is divided into a lower Ragdon Member and an upper Wistanstow Member in the immediate vicinity of the Onny Valley, but at Acton Scott the Henley Member calcareous sandstones replace most of the Wistanstow Member.

The sequence comprises five Caradoc Stages: Longvillian, Woolstonian, Marshbrookian, Actonian and Onnian. The Woolstonian is new and replaces the old Upper Longvillian Substage, whilst the Longvillian is redefined to replace the old Lower Longvillian Substage. The Marshbrookian/Actonian boundary is redefined to coincide with a major faunal turnover 10 m from the summit of the Crosspipes Member of the Cheney Longville Formation. North of the Stretton Hills, near Chatwall, the middle and upper Caradoc rocks differ from the southern sequence. Four formations are defined; in ascending order the Chatwall Sandstone Formation, Chatwall Limestone Formation, Cheney Longville Formation and Acton Scott Formation. This sequence ranges from Soudleyan to Actonian; no Onnian rocks are developed. Correlation between the northern and southern areas is difficult. A condensed sequence or non-sequence at the base of the Alternata Limestone Formation in the Onny Valley is not represented northwards. Correlation based on the identification of a transgressive impulse at the base of the Woolstonian in the Onny Valley suggests that the base of the Cheney Longville Formation at Chatwall may be slightly older than in the southern region, and the Chatwall Limestone Formation may be slightly older than the Alternata Limestone Formation, although their faunas are similar. Faunal lists are provided, including ranges, to facilitate correlation with the type area.

The brachiopod fauna, mainly internal moulds, consists of 63 species and subspecies – 17 Inarticulata, 31 Orthida, 14 Strophomenida and one Spiriferida. The following species are new: *Obolus salopiensis*, *Palaeoglossa lockleyi*, *Paracraniops doyleae*, *Schizocrania hewardi*, *Orbiculoidea ovata*, *Rhactorthis actoniae*, *Rhactorthis grandis*, *Bancroftina hewitti* and *Bancroftina whittingtoni*. New subspecies are *Dalmanella multiplicata prima* and *Dalmanella unguis ultima*.

Introduction

The abundant and well-preserved shelly fauna of the type Caradoc area, Salop (Fig. 1), represents a range of near-shore to off-shore environments and is ideal for the study of evolutionary ecology. However, before the ecology can be analysed successfully, it is necessary to revise the stratigraphy and also the systematics of the most common animal group – the Brachiopoda. This paper is chiefly concerned with the upper part of the type Caradoc succession, from the base of the Alternata Limestone upwards. However, in the area around Chatwall the stratigraphy of the middle Caradoc sediments is particularly complicated (Dean 1960a, Greig *et al.* 1968, Hurst 1979), and so it has been necessary there to revise the immediately underlying Longvillian strata as well. Dr M. G. Lockley is making a similar study of the older part of the type Caradoc.

Historical review

Murchison (1839) erected the name Caradoc for the Ordovician rocks of south-east Salop and applied the name Caradoc Sandstone to strata between the Wrekin and Coston (Figs 1 and 2).

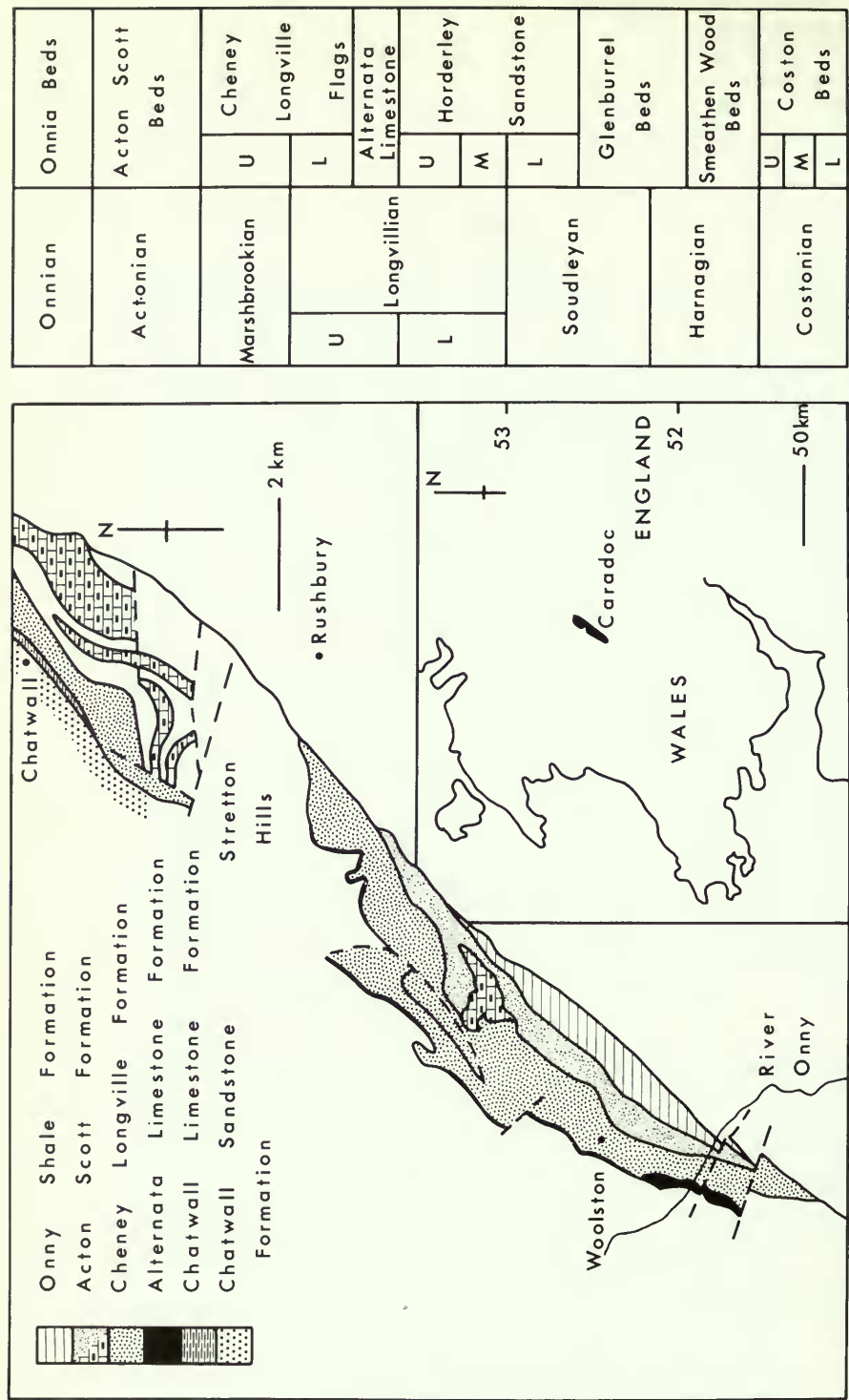


Fig. 1 Outline geological map of the area between Chatwall and Cheney Longville, showing the upper Caradoc rocks. Inset map shows the location of the Caradoc district. The stratigraphical column indicates the main lithological and chronological subdivisions of the whole Caradoc sequence, prior to this work.

CARADOC SANDSTONE		Murchison 1839	Salter & Aveline	La Touche	Lap. & Watts	Lapworth 1916	Bancroft 1929-1933	Dean 1958-1964	Hurst (this paper)
	Thinly	Thinly	Tri-nucleus Shales	Onny Shales	Tri-nucleus or Onny Shales	Upper Trinucleus Beds	Onny Shales	Onnia Beds	Onny Shale
	Lamin.	Lamin.			Onny Shales	Acton Beds	Acton Beds		Formation
	Sandy Shales	Sandy Shales	Thin bedded	Cheney	Acton	Acton Calcareous Beds	Calcareous Mudstones	Grey Mudstones and Limest.	Wistanstown Henley Member
									Acton Formation
	Fine grained	Fine grained	Long-village	Long-village	Cheney	Lower Trinucleus Shales	Transition bed	Upper Cheney	Crasspipes Member
	flaglike	flaglike			Long-village	Birrells Wood Flags	W. unguis Beds	Langville Flags	
	Sandst.	Sandst.	Flags	Flags	Long-village	Chelmick Flags and Shales	H. praeculta Beds		Cheney Longville Formation
							W. watissi Beds		
							K. geniculata Beds	Lower Cheney	Glynbara Member
							Laminated Flags	Langville Flags	
							H. alternata Beds	Alternata Limestone	Alternata Limestone Formation
	Siliceous Sandst.	Siliceous Sandst.	Chat-wall Sandst.	Horderley Sandst.	Chat-wall	Alternata Limestone	Lower Middle		
					Longville Group	Upper	Horderley Sandstone	Horderley Sandstone	Horderley Sandstone Formation

Fig. 2 The main classifications and correlations of upper Caradoc strata.

He stated that the Onny Valley presented the best section and as can be seen from Fig. 2 an attempted subdivision of the strata was made. However this unit was far more comprehensive than Murchison probably intended, as subsequent researchers showed it to contain rocks Pre-Cambrian to Silurian in age. Later Ramsay & Aveline (1848) and Forbes (1848) still retained the Upper Llandovery rocks of the Longmynd area in the Caradoc. Not until the work of Sedgwick (1852) was there realisation of the inherent mixture in the Caradoc. He noted the trilobites *Ampyx* and *Trinucleus* near Cheney Longville and differentiated the 'Horderley' and 'May Hill' (now Upper Llandovery) Caradoc faunas, suggesting that the latter were younger.

Ramsay (1853) revised his earlier interpretation (Ramsay & Aveline 1848), connecting the Caradoc Sandstones of the Longmynd with the Wenlock Shales. This small paper heralded the major changes of the following year, in which Salter & Aveline (1854) published their classic results. They divided the revised Caradoc Sandstone into five parts, from youngest to oldest:

1. *Trinucleus* Shales
2. Thin-bedded flags of greenish sandstone
3. Thick-bedded flags of Horderley
4. Hoar Edge Grits
5. Shales of Harnage and Shineton.

The first three units are the ones dealt with here (Fig. 2).

Callaway (1877) differentiated the Caradoc Harnage Shales from the Tremadoc Shineton Shales, placing the former above the Hoar Edge Grits. He also proposed the name Chatwall Sandstone to replace the 'thick-bedded flags of Horderley' of Salter & Aveline. In 1884 La Touche introduced the names Onny Shales, Cheney Longville Flags and Horderley Sandstone corresponding respectively to units 1 to 3 of Salter & Aveline (Fig. 2). From this it is apparent that the Chatwall Sandstone and Horderley Sandstone are synonymous. Lapworth & Watts (1894) subsequently erected Acton Scott Beds for strata contained between the Onny Shales above and the Cheney Longville Flags below (Fig. 2). Cobbold (1901) recognized the *Alternata* Limestone for the first time but placed it in with the Chatwall or Soudley Sandstone. With the coining of the term Soudley Sandstone, there were three names for a single unit, i.e. Chatwall, Horderley and Soudley Sandstones.

Lapworth (1916) proposed the name Caradoc Series and divided the strata into a number of 'Groups' (Fig. 2). These 'Groups' were further subdivided, but no information regarding lithologies, faunas or type localities was offered. Nevertheless, Lapworth was the first person to recognize the heterogeneous nature of the Cheney Longville Flags by subdividing the unit into three.

Bancroft subdivided the type Caradoc Series into units characterized by the faunas, mainly of brachiopods and trilobites (Fig. 2). He first named the Soudleyan, Longvillian and Marshbrookian Stages in the predominantly sandstone units in the middle of the Series (1929*a*). Later the same year (1929*b*) he listed six stages for the whole Caradoc, in ascending order Girvanian, Harnagian, Soudleyan, Longvillian, Marshbrookian and Actonian (Fig. 1). At this point the youngest stage, the Onnian, was not introduced by name, although the subdivision was incorporated in his table. Bancroft also privately published a short paper in 1933, showing the vertical extent and lithological and faunal composition of the Stages Costonian to Onnian. The Costonian was not defined and was simply introduced as a replacement for the Girvanian (Fig. 1).

A paper published posthumously (Bancroft 1945) added more information regarding the Stages, but unfortunately they still remained ill-defined in terms of vertical extent. Further, many of the subdivisions were defined before the species of brachiopods and trilobites upon which they depended had been formally erected. These inconsistencies have marred Bancroft's work and made it difficult to follow. Nevertheless, as Dean (1958) indicates, Bancroft revolutionized stratigraphical research in the Ordovician. Not only did he collect faunas in bulk from single horizons, but he also tried to introduce statistical methods into his palaeontological work (Bancroft 1928*a*), and his methods far surpass many of today.

Dean (1958, 1960*a*, 1964) reviewed and revised the Stages and Zones of Bancroft based on a thorough redescription of the trilobite faunas (Dean 1960-63) and also published extensive faunal lists, but did not formally revise the lithostratigraphy (Fig. 2). He suggested that the name Acton Scott Beds *sensu stricto* should be reserved for the yellow calcareous sandstones of the

CHRONOSTRATIGRAPHY		LITHOSTRATIGRAPHY		BIOSTRATIGRAPHY	
Series	Stage			Brachiopods	Trilobites
C O D A R A D O C	U p p e r	Onny Shale Formation		Onniella Sericaidea	Onnia
		Acton Scott Fm.	Wistanstow Member	Onniella Cryptothyris	Platylichas
			Henley Member		
			Ragdan Member	Onniella Hedstraemina	Chasmaps
		Cheney Longville Fm.	Crasspipes Member	Dalmanella	Braeggeralithus
			Glynbara Member	Kjaerina Bancraftina	
C	Lr	Alternata Limestone Formation		Heterarthris	
		Horderley Sandstone Formation			

Fig. 3 Revised stratigraphical classification of the type upper Caradoc Series.

Acton Scott district, whilst he referred to the time-equivalent division elsewhere simply as 'grey mudstones and limestones' (Dean 1958). The Geological Survey of Great Britain (Greig *et al.* 1968) essentially followed the previous nomenclatures, although they amalgamated all the facies of the Actonian into an Acton Scott Group, and did not subdivide the Cheney Longville Flags.

Lithostratigraphy: Cheney Longville to Soudley

The lithostratigraphical units recognized here are essentially those of Bancroft (1929*a, b*, 1933) and Dean (1958, 1964). However, it has proved desirable to revise some of the lithostratigraphic boundaries, as well as to formalize the nomenclature and to define boundaries precisely (Fig. 3). The stratigraphy of the Soudley to Cheney Longville area will be described first, followed by a short account of the Cardington - Chatwall district (Fig. 1).

a. Horderley Sandstone Formation

This formation immediately underlies the Alternata Limestone Formation from Soudley (SO 477918) to Cheney Longville (SO 415852). It has a maximum thickness of 180 m, in the Onny Valley (SO 415858), and consists of laminated and cross-bedded medium-grained sandstones (Fig. 16, p. 213). The basal beds are some 70 m thick and commence with laminated medium-grained sandstones which pass gradationally from the underlying Glenburrell Beds (Dean 1964). Interbedded shale units are common and may reach 10 cm in thickness. The middle part of the sequence is well exposed in the Long Lane Quarries (SO 413842) and the large Onny Valley Quarries (SO 415858), and consists of 50 to 60 m of massive, low angle cross-laminated or parallel-laminated medium-grained sandstone (Figs 19, 21). Shelly coquinas are common in the laminated sandstones, often reaching a thickness of 50 cm. The uppermost 30 or 40 m of this formation is only developed in the Onny Valley, and consists of parallel to very low-angle cross-laminated medium-grained sandstone. Interbedded thin bioturbated fine sandstones (*c.* 5 cm) occur in the upper 5 m and form a transition into the overlying Alternata Limestone Formation.

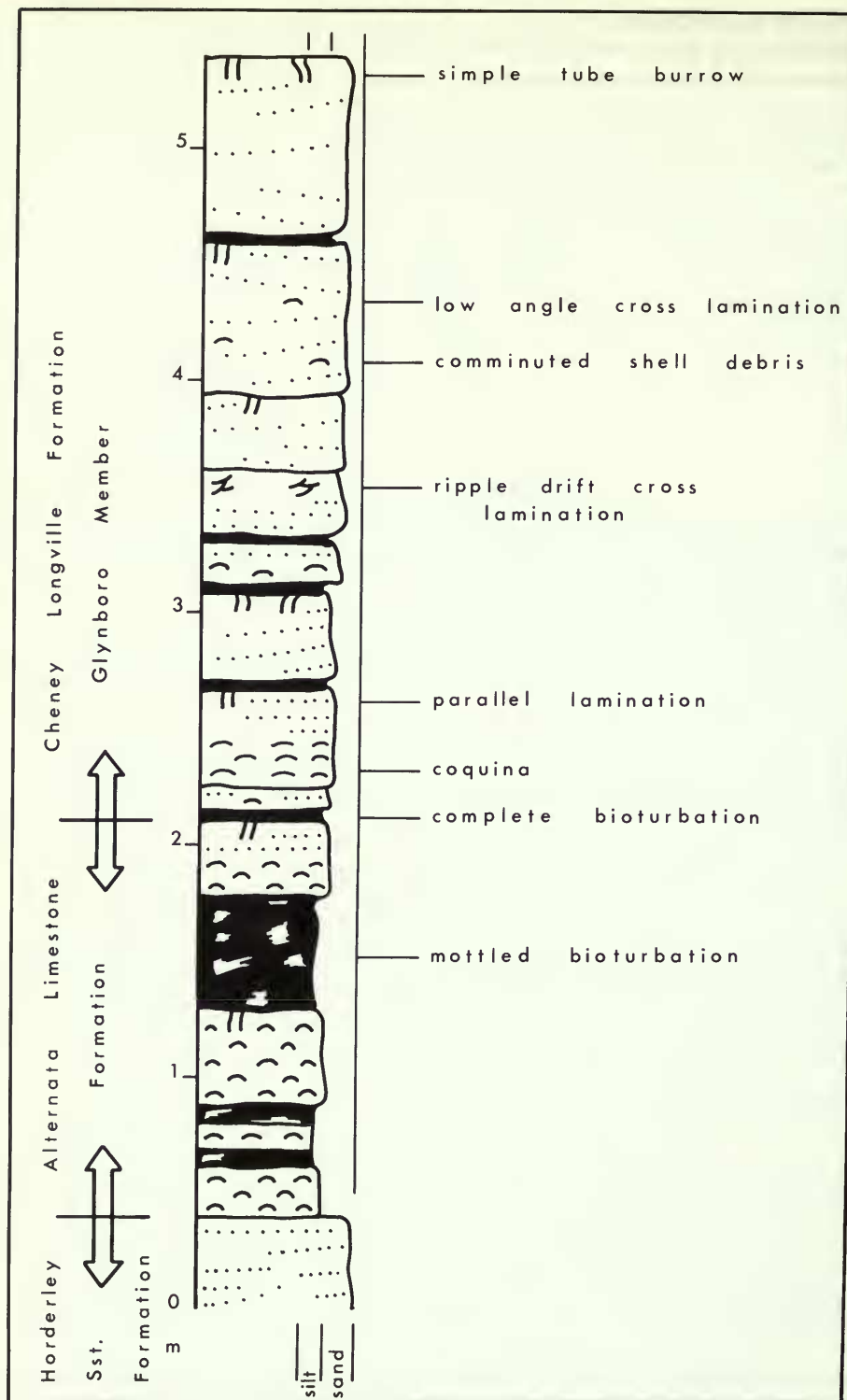


Fig. 4 Sedimentological log of the boundary between the Alternata Limestone Formation and Cheney Longville Formation at Soudley Quarry, SO 477918.

To define a lower lithological boundary to this formation, or to subdivide it, is outside the scope of this paper. However, an upper boundary is defined since it is also the base of the Alternata Limestone Formation.

Some 10 m west of a footbridge across the Onny River (SO 418856) the contact between the Horderley Sandstone Formation and the Alternata Limestone Formation is exposed. The top of the Horderley Sandstone Formation is defined at the base of the first thick shelly limestone influx (coquina) containing *Heterorthis alternata*, *Trematis punctata* and occasional phosphatic nodules and fossils (see Fig. 12, p. 202). In this section the initial coquina is some 50 cm thick, and occurs on both sides of the river bed. This section is also described below as the standard section for the base of the Woolstonian Stage (Fig. 12).

North of the Onny Valley in Marshbrook Railway Cutting (SO 440905) a faulted outcrop of the Horderley Sandstone Formation and Alternata Limestone Formation is seen. The contact is not now accessible (see Hurst 1979), but from the available exposure the Horderley Sandstone Formation does not appear to be as complete as in the Onny Valley. It consists of approximately 15 m of laminated medium-grained purple or greenish sandstone with thin shelly lenses along the laminae and with occasional pebble stringers 1 cm thick. These sediments are most similar to the middle or upper part of the Onny Valley sequence and there does not appear to be a gradation into sediments typical of the upper Horderley Sandstone Formation of the Onny Valley or into the overlying Alternata Limestone Formation.

At Soudley Quarry (SO 477918) parallel-laminated medium-grained purple and green sandstones with occasional thin shelly layers (Fig. 16) are overlain by the Alternata Limestone Formation (Hurst 1979). This is presumably one of the localities that prompted Cobbold (1901) to refer to a 'Chatwall or Soudley Sandstone'. As Dean (1960a) has demonstrated and will be discussed later, the Chatwall Sandstone is a lithostratigraphic unit distinct from the Soudley Sandstone. However, there is no lithological difference between the Horderley Sandstone Formation and Soudley Sandstone. Thus the term Soudley Sandstone is abandoned in favour of the Horderley Sandstone Formation, which has priority.

b. Alternata Limestone Formation

This stratum is named after the brachiopod *Heterorthis alternata* which occurs abundantly in shelly limestone lenses (Fig. 24). Cobbold's name (1901) is retained because the index species *Heterorthis alternata* is the type-species of the genus and the Alternata Limestone Formation includes the type-locality for the species.

The Alternata Limestone Formation consists of a series of interbedded bioturbated silty shales and sandy silts (c. 10 cm), laminated and graded fine sandstones often with a basal shell lag (10 to 50 cm thick), and thick shelly limestone bands (Fig. 22). The latter can be 50 cm thick, and consist of packed coarse shell material set in a matrix of sandy silt. The shells show no signs of grading or preferred orientation, but the beds appear crudely laminated owing to the alignment of large flat shells of *Heterorthis alternata* and *Kjaerina bipartita* (Fig. 24).

As Dean (1958, 1964) pointed out, this formation is a useful mapping horizon at the base of the Cheney Longville Formation. Nowhere does it exceed 30 m in thickness, and its maximum development is at Woolston (SO 423873). Between the roadside exposure west of Cheney Longville (SO 416852) and the Onny Valley (SO 418856 and SO 418857) it maintains a thickness of approximately 20 to 25 m. At Marshbrook (SO 440905) only some 15 m are exposed but its true thickness is probably greater than this. Only 2 m of Alternata Limestone Formation occurs at Soudley Quarry (SO 477918). This small thickness, and the fact that phosphatic nodules and phosphatized fossils also occur, suggests a condensed sequence (Fig. 16). Between Soudley and Cheney Longville it is only the basal metre of the succession which contains phosphatized fragments. An analysis of the facies changes at this horizon, with detailed sections, are given by Hurst (1979). Discussion of section correlations of the uppermost Horderley Sandstone Formation and Alternata Limestone Formation are given later under Chronostratigraphy, p. 210.

Soudley Quarry (SO 477918) is the only place where the contact of the Alternata Limestone Formation and the Cheney Longville Formation is seen. This is not the ideal locality to define the junction of these two formations. However, in the Marshbrook (SO 440905), Woolston (SO

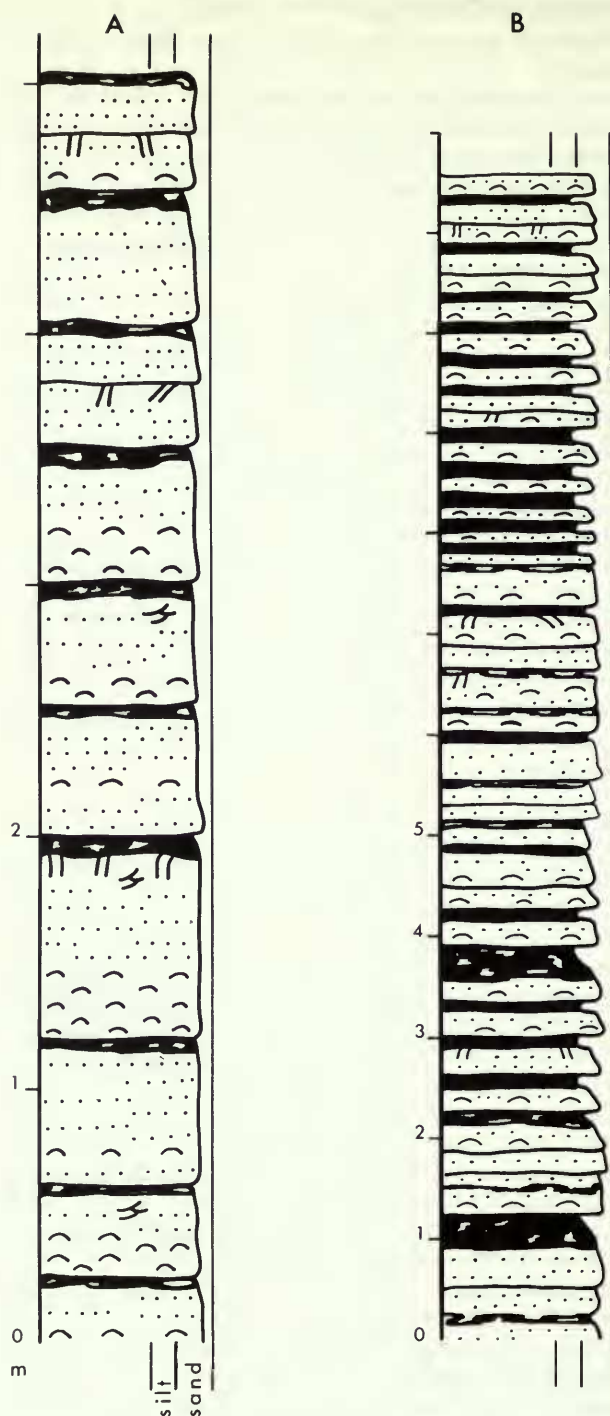


Fig. 5 Examples of sedimentary logs of the Glynboro Member of the Cheney Longville Formation, from (A) the stream section at Soudley SO 478916 and (B) the old river cliff locality in the Onny Valley at SO 422890. Symbols explained in Fig. 4.

423873) and Onny Valley (SO 418857) sections there is a gap, of 5 to 10 m stratigraphically, between the highest undoubted Alternata Limestone Formation exposure and lowest strata of the Cheney Longville Formation. As can be seen from Fig. 4, p. 190, the basal Cheney Longville Formation is readily distinguishable from the Alternata Limestone Formation. The top of the latter is taken to coincide with the top of the last thick shelly limestone coquina with abundant *Heterorthis alternata*. Above this the Cheney Longville Formation is characterized by the absence of shelly lenses, and the sediment is also slightly coarser.

c. Cheney Longville Formation (Figs 17, 18, 20)

The Cheney Longville Formation is an homogeneous sequence of sands, silts and sandy silts, some 180 to 200 m thick and weathering greenish-yellow. It was originally named by La Touche (1884), Fig. 2. Two members are recognized.

Glynboro Member. The basal member, named after the cottage of Glynboro (SO 418859) in the Onny Valley, corresponds precisely to the Lower Cheney Longville Flags of Dean (1958). It comprises approximately 120 m of buff yellowish to olive green weathering siltstones and sandstones. Sandstone beds 10 to 50 cm thick are interbedded with 20 cm bioturbated sandy silt units (Fig. 17). The sandstone beds are graded and have planar erosive bases and occasionally a persistent basal coquina which gradationally passes up into parallel or very low-angle cross-lamination. The bioturbated horizons account for approximately 10% of the succession in the lower half of the Member and up to 25% in the upper part. The fauna is best in the coquinas, but occurs as comminuted debris throughout. A very sparse fauna occurs in the bioturbated horizons and is the same species as in the shell beds. An example of a sedimentary facies log of this member is shown in Fig. 5 (see also Hurst 1979).

The base of the Glynboro Member and the Cheney Longville Formation is defined at Soudley Quarry (Fig. 4). Very few good sections exist in the lowest part of this Member, the most extensive being in the stream section (SO 478916) south-west of Soudley Quarry (see Hurst 1979). Poor sporadic exposures occur in the lane west of Cheney Longville and in the Onny Valley. The higher beds are better represented. An almost continuous laneside exposure due west of Cheney Longville (SO 418851) includes the transition into the overlying Crosspipes Member. Further limited exposures occur at Woolston, and in an old cart track at Whittingslow (SO 436892) there is another continuous exposure into the Crosspipes Member. An extensive section is present in an old river cliff in the Onny Valley (SO 422890).

Crosspipes Member. This member, named after Crosspipes Farm (SO 429892), comprises a maximum of 60 m and corresponds to the Upper Cheney Longville Flags of Dean (1958). It consists of thin laminated and graded very fine sandstones (c. 10–15 cm) interbedded with thick (up to 50 cm) bioturbated sandy and silty shales (Figs 18, 20). The tops of the fine sandstone beds are penetrated by simple tube burrows and grade into the overlying bioturbated units. Fauna is abundant in the bioturbated units and the same species occur concentrated as lensing shell lags at the base of the laminated sandstones (Fig. 25). Some lenses are up to 15 cm thick and are persistent. Occasionally in the bioturbated silty shales thin lenses of small fragments of volcanic glass, pumice and orthoclase feldspar crystals can be traced across the outcrop.

The thickness of the laminated fine sandstones decreases quickly up through the member until the top 10 or 15 m consists primarily of bioturbated and partially bioturbated sandy silts and sandy shales. Shell concentrations up to 5 cm thick become common in the top 10 m of strata, but they are not associated with laminated graded sand units (Fig. 18). Fig. 6 gives examples of sedimentary logs from this member.

The Crosspipes Member (lowest part) is well exposed at the motte and bailey at Cheney Longville (SO 419849), in an extensive river section in Marshwood (SO 442891) and a river section near Ragleth Hill (SO 451908).

The base of the Crosspipes Member, and thus the top of the underlying Glynboro Member, is taken in a fairly continuous roadside exposure at Cheney Longville (SO 418851 to SO 419849), and coincides with the stage boundary between the Woolstonian and the Marshbrookian (Fig. 13,

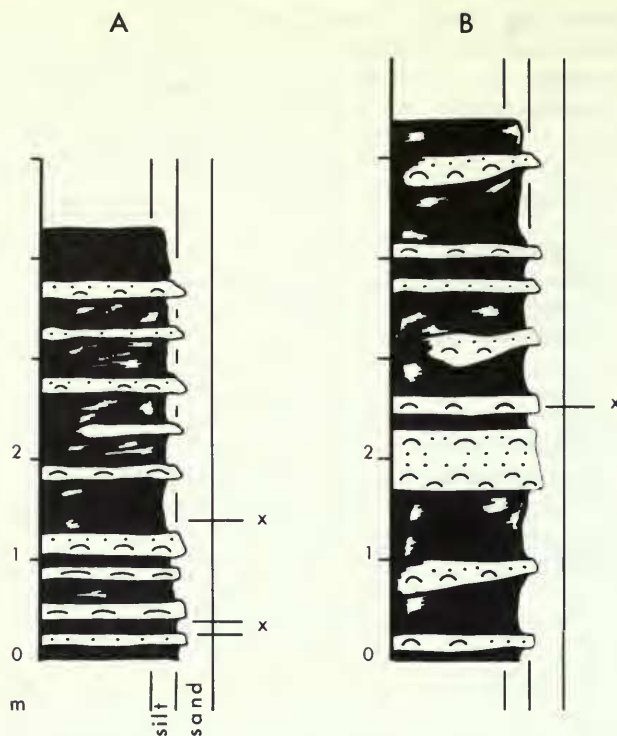


Fig. 6 Examples of sedimentary logs of the Crosspipes Member of the Cheney Longville Formation, from (A) the Minton road section at SO 439900 and (B) the stream section in Marshwood at SO 422891. Symbols explained in Fig. 4.

p. 203). The lithological boundary between the two members is gradational over several metres. The base of the Crosspipes Member is taken at the increase in thickness of bioturbated units intercalated with thin laminated sandstone beds. This change is also accompanied by a decrease in sediment grain size from predominantly sands and sandy silts to silts and silty shales (Fig. 20). The fauna is also more abundant in the Crosspipes Member.

d. Acton Scott Formation

In the Onny Valley above the Cheney Longville Flags and below the Onny Shale Formation (Fig. 3) the sequence consists of two basic facies, a siltstone below and a calcareous siltstone above. However, to the north, around Acton Scott, the siltstones are succeeded by hard calcareous sandstones. Each of these three divisions is defined here as a member.

Ragdon Member. Named after the village of Ragdon (SO 458915), this comprises approximately 30 m of mottled (intensely bioturbated) siltstones, weathering buff to green. Occasionally burrow-disrupted current laminae occur, and non-bioturbated primary bedding accounts for about 2% of the succession. Isolated laminated siltstone beds with a basal layer of shell debris occur rarely. The rich and diverse fauna is distributed randomly throughout the sequence, although paper-thin layers of bedding-parallel shell fragments and convex-upward shells (not associated with laminated silts) occur at a frequency of about one layer per 5 m (Fig. 26).

This member weathers easily to form low-lying land, and as a result is poorly exposed, mainly in overgrown stream sections. It is not exposed south of the Onny Valley; a stratigraphically low but poor exposure under a tree in an abandoned meander of the river is the most southerly outcrop (SO 423854). Two small outcrops in the middle part of the member occur on the north side of the river in a roadside bank (SO 424855) and in an overgrown valley known as Dandy Hollow

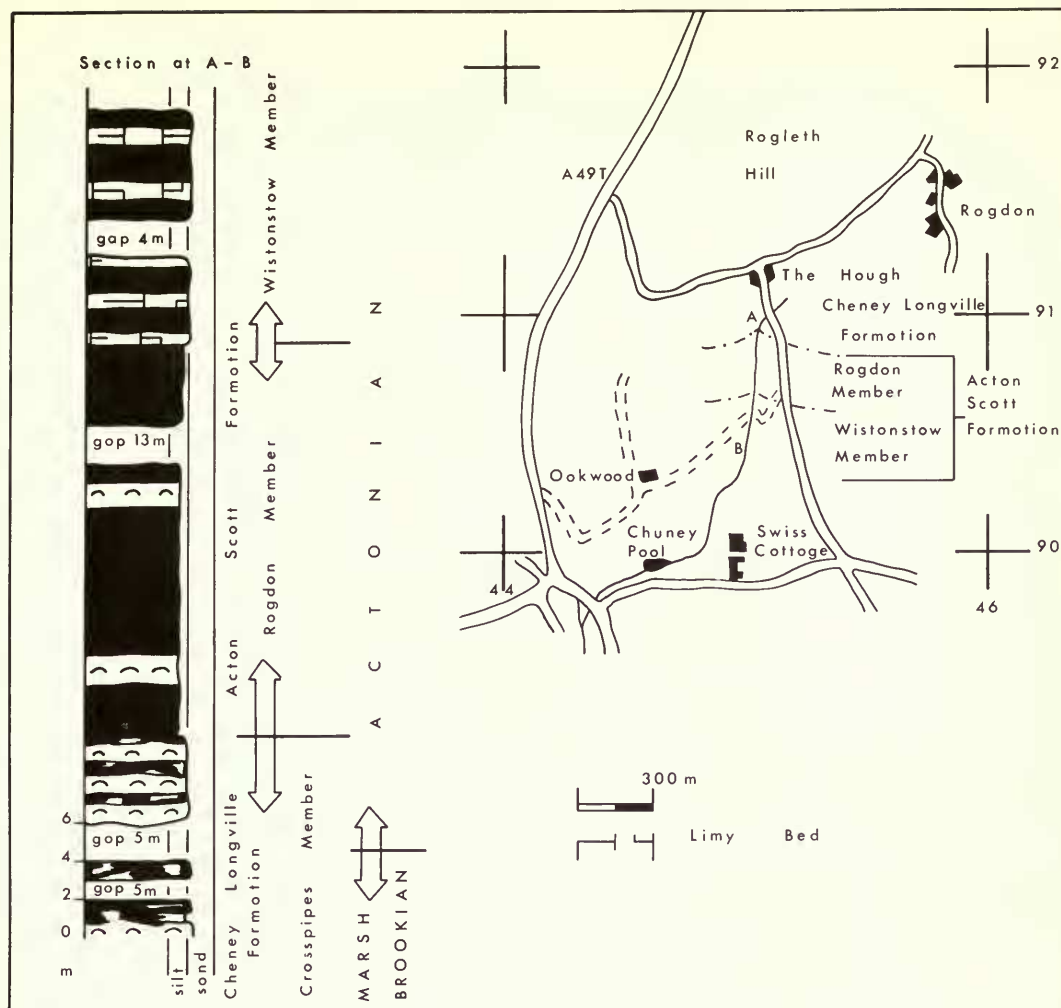


Fig. 7 Location of the stratotype boundary between the Cheney Longville Formation (Crosspipes Member) and the Acton Scott Formation (Ragdon Member), and between the Ragdon and Wistanstow Members of the Acton Scott Formation. Symbols explained in Fig. 4.

(SO 425858). Dean (1958) reported that in Marshwood Quarry (SO 445890) the transition from the Cheney Longville Formation to the Acton Scott Formation could be examined in the cart track to the south, but this is not possible now as the section is overgrown. In the vicinity of Acton Scott there are stream exposures at Ragleth Hill (SO 451906), west of Hatton (SO 465901) and at Chune Pool (SO 466899).

The only exposure of the transition from the Cheney Longville Formation (Crosspipes Member) to the Acton Scott Formation (Ragdon Member) is in a stream section near Oakwood south of Ragleth Hill (SO 451908 to SO 451906), and this is considered the stratotype between the two formations and their members (Fig. 7). The boundary is gradational over a couple of metres, the sediment grain size changing from a sandy silt to a muddy silt. The boundary is taken at the beginning of the finer-grained sediments, which are more mottled and thoroughly bioturbated. This transition is accompanied by a loss of distinct shelly layers (Fig. 7). Detailed work by Bancroft in the Onny Valley indicated a complete section in this interval (SO 422854). However, the section is not now so clean (see Fig. 8), but various small pits were dug and a similar transition as described for the type section was verified.

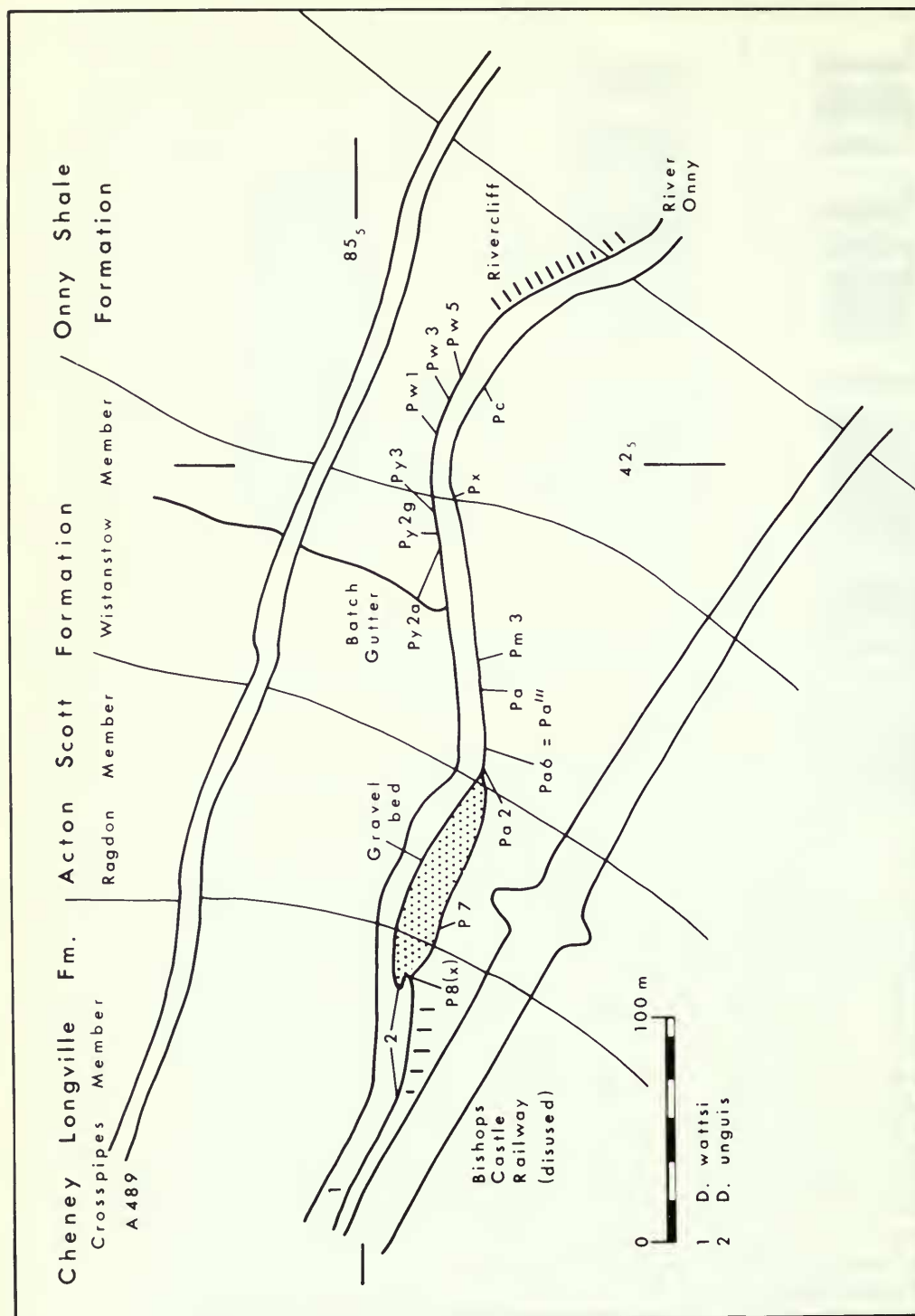


Fig. 8 Upper Caradoc exposures in the Onny Valley section. The numbered localities are from Bancroft (1949), most of which are still extant, except for P8(x) and Px. The point between Py3 and Px marks the stratotype between the Acton Scott Formation (Wistanstow Member) and the Onny Shale Formation as well as between the Actonian and Onnian Stages.

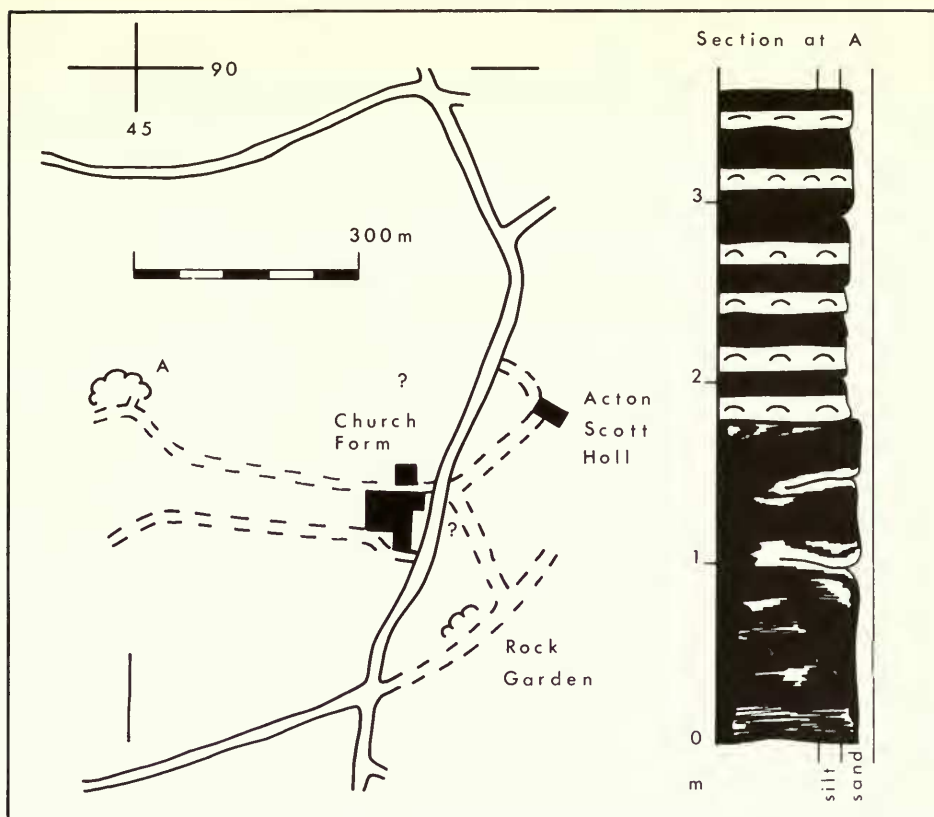


Fig. 9 Location and section of the stratotype for the Henley Member of the Acton Scott Formation. Symbols explained in Fig. 4. Question marks indicate filled-in quarries.

Wistanstow Member. Named after the village of Wistanstow 500 m north of the Onny Valley, this consists of some 40 m of thoroughly bioturbated yellowish to blue weathering calcareous siltstones and blue-black silty mudstones. Gradational silty blue limestone bands and nodules occur throughout. Generally the fauna is of low diversity although occasional thin bedding planes contain locally concentrated convex-upward shells.

Near Acton Scott the member is far more silty and contains thick (c. 10–15 cm), hard, somewhat nodular blue limestone bands (Fig. 7). In the stream section south of Ragleth Hill (SO 451905) some 5 to 10 m is exposed above the Ragdon Member, and a similar smaller sequence is exposed at the top of the section in the river west of Hatton (SO 465901). In the Onny Valley the sediments are finer and consist of silty muds (see Fig. 8). Persistent limestone bands are not present, but scattered discrete nodules are common. Dean (1958) reported blue calcareous mudstones in a stream section at Ticklerton (SO 479910), which belong to the Wistanstow Member and which Dean considered to be middle Actonian.

The base of the Wistanstow Member is only exposed in the stream section at Oakwood (SO 451908 to SO 451906), and this is made the type locality for the junction between the Ragdon and Wistanstow Members of the Acton Scott Formation (Fig. 7). The sediment grain size is somewhat gradational over a metre, changing from muddy silts to sandy silts. However the base is defined by the incoming of thick, conspicuous, blue limestone bands which can be traced across the outcrop. They contain a rich fauna but the intervening bioturbated beds are only sparsely fossiliferous.

Henley Member. This unit, named after the village of Henley (SO 451883), is a hard calcareous sandstone which forms the high ground around Acton Scott. The beds immediately above and

below the sandstone are not exposed and its thickness is not precisely known, although Greig *et al.* (1968) estimated it to be about 25 m.

The type section for this unit is taken to be the old quarry west of Acton Scott (SO 449896). Here some 5 or 6 m of massive yellow-weathering calcareous medium-grained sandstone, with a low diversity and density fauna, is succeeded by thinly-bedded bioturbated calcareous sandstones above (Fig. 9). The fauna in the upper unit is very diverse and commonly concentrated along thin bedding planes. Other exposures of this unit include the rock garden at Acton Scott Hall (SO 454893). Here the sandstone is lithologically different from the type section in that it is more muddy, resulting in a general blue colour. The boundaries of the member are not exposed.

e. Onny Shale Formation

This formation is a distinct lithological unit at the top of the Caradoc succession. The name Onny Shale is preferred to *Onnia* Beds of Dean (1958) not only because it has priority but also because it can be recognized on lithological grounds alone. The formation only outcrops in the Onny Valley (see Fig. 8) and consists of approximately 45 m (exposed) of mudstones at the type section (SO 425854 to SO 426854), which fall into three facies.

a. 20 m of bioturbated blue-black mudstones with individual lithified burrows. Some small pyritic nodules occur. A low-diversity but dense fauna is present, but is often crushed owing to sediment distortion.

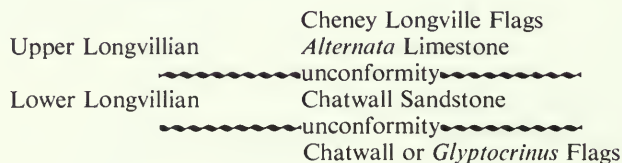
b. 5 m of laminated blue-grey shale occurring in the river bed, just before the famous river cliff section (SO 426854) which forms the uppermost facies. It is similar in texture and composition to the mudstones, except that bioturbation is absent or restricted to single tube burrows. Laminae are on a millimetre scale and are defined by variations in the mud, silt and clay content of the sediment. Benthic fauna is extremely rare, but pelagic graptolites occur.

c. The river cliff section which consists of yellow-weathering blocky mudstones with restricted benthic fauna.

3 m is not exposed at the junction of the Acton Scott Formation (Wistanstow Member) and the Onny Shale Formation (Fig. 8). This (SO 425854) is taken as the type section for the boundary and within the missing sequence the poorly fossiliferous nodular calcareous muds and silts of the Wistanstow Member are replaced by the bioturbated blue-grey, pyritic, very fossiliferous muds of the basal Onny Shale Formation. The top of this formation is unconformably covered by the Llandoverly.

Lithostratigraphy: Cardington to Chatwall

North of the Stretton Hills the lithostratigraphical succession of the middle, and parts of the upper Caradoc succession are different from the southern area. Dean (1960a) presented a detailed analysis of the Caradoc strata up to and including the *Alternata* Limestone. The succession he employed for this interval is as follows.



Dean's unconformities are based entirely on faunal evidence and represent missing faunal assemblages (zones) compared with the Onny Valley section. Hurst (1979) has analysed the environment of deposition of the *Alternata* Limestone Formation and suggested that the unconformities may not be present. The evidence for this is discussed later under section correlation, p. 216. Only the strata above and including the Chatwall Sandstone are dealt with here, and a different lithostratigraphical nomenclature is required for this area, reflecting localized sedimentation patterns, a point also emphasized by Dean (1958, 1960).

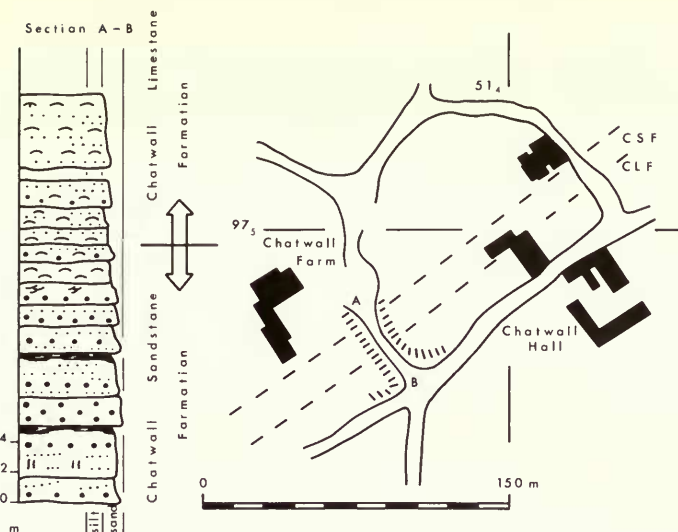


Fig. 10 Location and stratotype section for the Chatwall Sandstone and Chatwall Limestone Formations. Symbols explained in Fig. 4.

a. Chatwall Sandstone Formation

The Chatwall Sandstone Formation (Callaway 1877) is regarded as distinct from the Horderley Sandstone Formation and the name is used for strata north of the Stretton Hills (Fig. 1). The type section is taken in the lane to the south-west of Chatwall Hall (SO 514974), where are exposed some 18 m (Fig. 10) of lensing units of pebble conglomerates up to 100 cm thick, which are persistent across the outcrop. These pass sharply upwards into buff yellow, planar or low-angle cross-laminated, medium coarse sand units up to 150 cm thick. Some mottling is present (bioturbation) but body fossils have not been found in the lower 12 m, although Dean (1960a) reported occasional fragments. The uppermost 1 or 2 m has a fauna concentrated in shell lags. Pebble beds decrease in thickness and frequency into the upper part of the formation.

This definition of the Chatwall Sandstone Formation includes the lower 10 m which Dean (1960a) placed in the Chatwall Flags. The unit is exposed in numerous roadside cuttings, as the pebble beds form hard bands (SO 502965, SO 497961), and in some small quarries (SO 498962). The sandstone is hard and between Cwms and Chatwall caps an escarpment, but no base can be defined as exposure of this level is lacking.

b. Chatwall Limestone Formation

Formerly called the *Alternata* Limestone, it is not only readily distinguishable, lithologically, from the underlying Chatwall Sandstone Formation but also from the redefined *Alternata* Limestone Formation of the Soudley and Onny Valley region.

The type section is also located in the lane at SO 514974, where the limestone lies directly on the Chatwall Sandstone Formation (Fig. 10). The limestone consists of a matrix of medium-grained yellow sandstones which occur in laminated beds up to 50 cm thick. Fauna is common and concentrated in the base of individual beds or scattered throughout a unit. In many beds the shelly concentrates are so common as to form limestone bands. Occasional pebbles occur in the coquinas or are scattered along the laminae. Bioturbation is absent.

The base of the Chatwall Limestone Formation is defined in the lane section, and the transition is gradational over a metre. The base is taken at the first thick shelly coquina which contains *Heterorthis alternata*, accompanied by a reduction in sediment grain size and a loss of persistent pebble bands (Fig. 10). Away from the type section the limestone is now poorly exposed apart from a quarry in The Wilderness (SO 489956). A top to the Chatwall Limestone Formation cannot be defined as no suitable exposure exists.

c. Strata above the Chatwall Limestone Formation

In this northerly area the Cheney Longville Formation follows the Chatwall Limestone Formation, but it is very poorly exposed; the exposures that do exist confirm a similar sequence to the Soudley to Cheney Longville area.

The highest beds of the district belong to the Acton Scott Formation. Pocock & Whitehead (1948) stated that Lapworth's Acton Group did not occur north of the Cardington Hills. However, as Dean (1958) pointed out, the faunas recorded by Salter & Aveline (1854), from a fossiliferous locality near Gretton, indicate Actonian strata. More recently Greig *et al.* (1968) have reported some 160 m of strata which they refer to the Acton Scott Group, and which consists of two yellow flaggy shelly sandstones interbedded with mudstones. These beds are also considered here as the Acton Scott Formation, but the poor exposures preclude the erection of members. The increase in thickness of the formation from the Onny area is owing to the two sandstones which are lithologically similar to the Henley Member; the flaggy nature refers to the lamination. The reported fauna is also very similar.

Biostratigraphy

Bancroft (1928*b*, 1929*a, b*, 1933, 1945, 1949) revolutionized Caradoc stratigraphy by his erection of zonal schemes based on trilobites and brachiopods. Dean (1958) has revised some of this work, but without taxonomic revision of the brachiopods. Brachiopods are numerically the most important invertebrate group throughout all the formations (Hurst & Hewitt 1977) and the present revision of their taxonomy necessitates changes. As with the trilobites, genera often have fairly long ranges so that specific identification is critical.

The table at the end of this section (p. 207) shows the stratigraphical ranges of all the invertebrate species encountered in the upper Caradoc succession. It is suggested that the previous zonal schemes be abandoned (see Fig. 11). The concept of many of the brachiopod species is now radically different and many of the species names used by Bancroft are invalid. Over-emphasis of one particular species is also dangerous for correlation purposes. For these reasons the overall fauna should be used and in fact there are many faunal turnovers which not only reflect events controlled by ecological changes, but may be useful in correlation. Nevertheless, it is interesting that most of the zones of Bancroft (1933) do not simply reflect shifts of one or two species, but mirror major benthic events, affecting whole faunas. Characteristic species of upper Caradoc trilobites are shown in Figs 27–41.

The fauna of the Alternata Limestone Formation is dominated by brachiopods, which constitute upwards of 90% of the individuals. *Heterorthis alternata*, *Sowerbyella sericea*, *Trematis punctata*, *Bancroftina typa* and *Kjaerina bipartita* are the most common species, whilst trilobites are mainly represented by *Broeggerolithus longiceps*, *Kloucekia* (*Phacopidina*) *apiculata* and *Brongniartella bisulcata*. *Chasmops extensus* appears for the first time. The majority of the fauna occurs in shell beds and there is some indication that *H. alternata* and *T. punctata* occur together preferentially in particular beds (Hurst 1979). The total fauna is not diverse, which is not surprising as the sediments indicate nearshore environments (Hurst 1979). The abundance of both *H. alternata* and *T. punctata* forms a very useful marker horizon. The assemblage differs from the fauna in the uppermost Horderley Sandstone Formation (Onny Valley *sensu stricto*) in having these two species and also a far greater abundance of *Kjaerina bipartita*, which is of greater size in the Alternata Limestone Formation. *S. sericea* dominates the whole fauna of the underlying formation, whereas in the Alternata Limestone Formation it is not as common. The trilobite fauna is also different, with the main species in the Horderley Sandstone Formation being *Broeggerolithus globiceps*, *Brongniartella minor* and *Flexicalymene* (*Reacalymene*) *horderleyensis*. The latter two are rare, but the former is not uncommon.

The Glynboro Member of the Cheney Longville Formation contains two distinct faunal units. In the lower half the fauna is mainly left over from the preceding Alternata Limestone Formation, without *H. alternata* and *T. punctata*. The most abundant species are *Bancroftina typa* and *K. bipartita*. *S. sericea* again decreases in importance but the trilobite fauna is the same as previously,

STAGE	BANCROFT (1929b)	BANCROFT (1933)	LITHOSTRATIGRAPHY			
ONNIAN	Cryptolithus superbus	Onnia superba	Onny Shales			
	Cryptolithus gracilis	Onnia gracilis	Actan Scatt Beds			
	Cryptolithus cabbaldi	Onnia cabbaldi				
Resserella paracyclica	Onniella grandis					
Hedstraemina rabusta						
ACTONIAN						
	Kjerulfina palcyma	Onniella reuschi	Langville Upper			
	Wattsella unguis	Wattsella unguis				
Wattsella Heterarthina wattsi praeculta	Wattsella wattsi					
UPPER LONGVILLIAN	Kjaerina geniculata	Kjaerina geniculata			Flags Middle Lower	
	Kjaerina bipartita	Kjaerina bipartita				

Fig. 11 Previous zonal and stratigraphic schemes of Bancroft, 1928–49.

dominated by *Broeggerolithus longiceps*. The fauna is not diverse nor abundant and is mainly limited to shell beds. The upper half of the Glynboro Member contains a complex of new species. The most abundant species are the brachiopods *Kjaerina typa* and *Dalmanella multiplicata multiplicata*. *S. sericea* occurs in small numbers as well as *Paracraniops doyleae*. One of the most characteristic brachiopods of this unit is *Dolerorthis virgata*. It is never abundant but persistently present. An important local extinction is that of *Bancroftina typa*. Trilobites continue from below with little change, dominated by *B. longiceps*, but *Chasmops extensus* becomes more abundant. Other important faunal aspects include the increase in abundance of *Tentaculites anglicus* and the introduction of a few bivalves, notably '*Avicula*' *orbicularis*. The fauna of the upper part of the Glynboro Member is more diverse than the lower part.

The Crosspipes Member is only some 60 m thick, but three distinct faunal developments are seen. These correspond to the three original brachiopod zones, *Wattsella wattsi*, *Wattsella unguis* and *Onniella reuschi*, which Bancroft (1933) erected. The lowest fauna (c. 25 m of strata) consists of some species from the uppermost Glynboro Member but with important new elements. *Tentaculites anglicus* tends to dominate the fauna. As a group the brachiopods are still most abundant, such strophomenides as *Kjerulfina trigonalis* and *Strophomena grandis* being characteristic. Both of these are new to the area and they are never common, although persistent. The dalmanellid *Bancroftina hewitti* (reintroduction of the genus *Bancroftina*) and the heterorthisid *Heterorthis praeculta* are restricted to this faunal unit and, with abundant *Dalmanella multiplicata multiplicata*, characterize the whole assemblage. *Sowerbyella sericea* is more abundant than in the preceding assemblage. The most striking absentee from this unit is the *Kjaerina* species group, which does not reappear in the Caradoc succession. The top 3 m of this assemblage

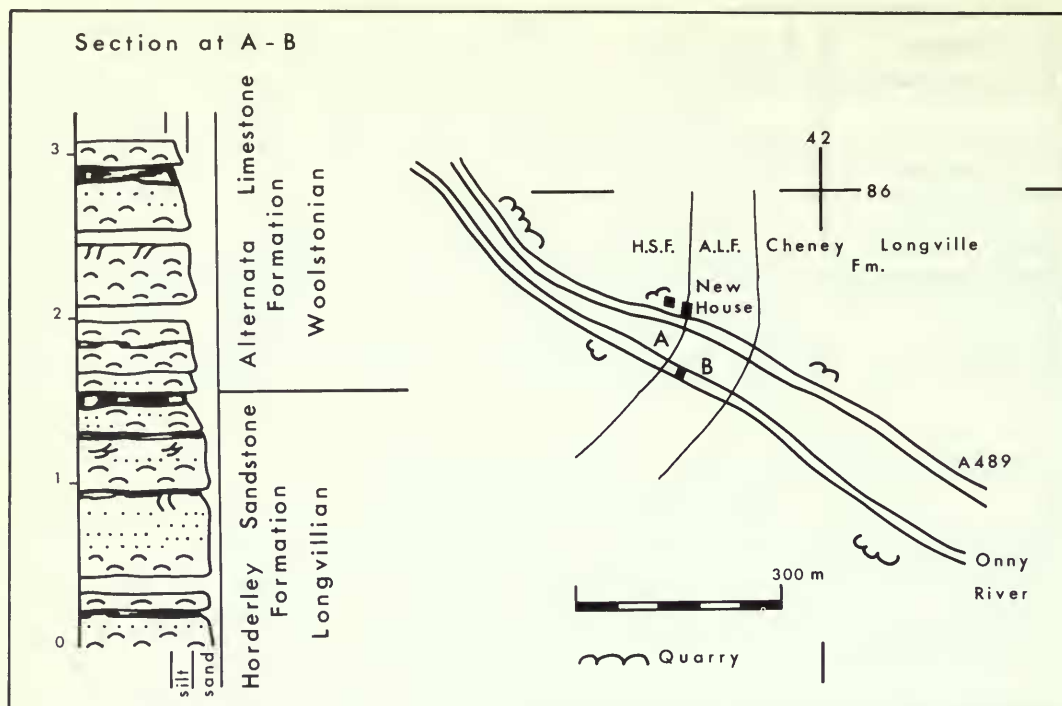


Fig. 12 Location and stratotype section for (1) the boundary between the Horderley Sandstone Formation and the Alternata Limestone Formation, and (2) the Longvillian and Woolstonian Stages. Symbols explained in Fig. 4.

is characterized by the abrupt disappearance of *D. multiplicata multiplicata* and its replacement by *Dalmanella watti*. *Heterorthis praeculta* is more abundant in this interval, which Bancroft originally termed the *H. praeculta* superzone.

Of the non-brachiopods a prasopodid bryozoan becomes common. The only new trilobite which is common and diagnostic of this assemblage is *Broeggerolithus transiens*. Other trilobites are similar to the preceding faunal assemblages, although *Brongniartella bisulcata* is uncommon but persistent, whereas *Chasmops extensus* and *Flexicalymene caractaci* increase in numbers. Bivalves are uncommon, but include small individuals of *Similodonta* sp. and *Nuculites planulatus*.

This assemblage is abruptly replaced by one dominated by *Dalmanella unguis* and *Tentaculites anglicus*; the latter reaches its acme in this fauna. Rarer but diagnostic species include *Strophomena grandis* and *Kjerulfina trigonalis* which persist from the basal assemblage, but become more abundant. This assemblage marks the first appearance of *Hedstroemina*, here *H. fragilis*, which is rare. Apart from *S. sericea* which is also rare, the remaining fauna is similar to the preceding assemblage. In the upper half of this subunit the total fauna becomes rarer and the brachiopod individuals, of every species, become smaller. Such changes presumably relate to a local ecological event.

The upper faunal assemblage (c. 10 m) is distinguished by both species introductions and local extinctions. *Tentaculites anglicus* becomes rare (Hurst & Hewitt 1977) as does *D. unguis*. Other reductions include *S. grandis*, whilst *K. trigonalis* is totally lost. A characteristic feature of the assemblage is the sudden introduction and dominance of *Onniella reuschi*. This is accompanied by the reintroduction of common *S. sericea*, a large increase in abundance of *H. fragilis*, often dominating single horizons, and the appearance of *K. polycyma*. Other introductions include *Rhactorthis grandis*, *Reuschella bilobata* (in abundance), *Horderleyella* cf. *plicata* and *Leptaena salopiensis*. Bryozoans increase in abundance and diversity as prasopodid, ramose and stick morphotypes become common. Bivalves are commonly represented by *Similodonta* sp. with less

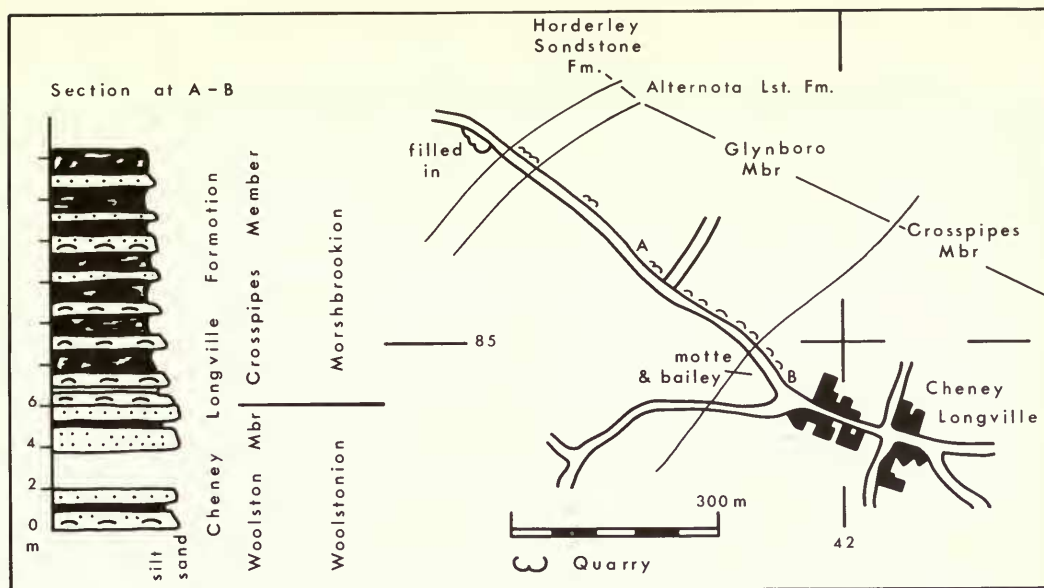


Fig. 13 Location and stratotype section for (1) the boundary between the Glynboro Member and Crosspipes Member of the Cheney Longville Formation, and (2) the Woolstonian and Marshbrookian Stages. Symbols explained in Fig. 4.

common '*Avicula*' *orbicularis* and *Nuculites planulatus*. Gastropods are not common and are often indeterminable, although apparently chiefly bellerophontaceans. The trilobite fauna appears similar in species composition to the underlying assemblage, but changes in abundance occur. *B. transiens* and *C. extensus* are rarer; the most common form is *Flexicalymene caractaci*. *Primasps caractaci* makes its first appearance. The upper assemblage is very diverse, with a more abundant fauna (high density) than the preceding faunal units. This assemblage also marks the initial shift in abundance changes for major taxa, for instance the bivalves and gastropods are numerically important for the first time; this trend continues into the units above (Hurst & Hewitt 1977).

Based on faunal differences, Dean (1958) subdivided the Acton Scott Formation of the Onny Valley into three. Here only a bipartite faunal division is recognized; the faunal assemblages correlating with the two member units of the formation. The lowest faunal assemblage, in the Ragdon Member, does not differ greatly in diversity and density from the preceding unit, and represents only a change in faunal emphasis. *Onniella reuschi* is still dominant, with other common forms such as *H. fragilis*, *L. salopiensis*, *Rhactorthis* cf. *crassa* and *R. bilobata*. *Kjerulfina polycyma* disappears but a few rare species like *Zygospira* sp., *Skenidioides* cf. *costatus* and *Obolus salopiensis* appear. *Cryptothyris paracyclia* and *Nicolella actoniae*, which become more abundant later, make their first tentative appearance. The most important brachiopod introduction is *Chonetoidea radiatula* which is abundant and diagnostic.

Trilobites are not common, but include *Flexicalymene laticeps*, *Primasps caractaci* and *Calyp-taulax actonensis*. The most important feature of this faunal unit is the increase in molluscan numbers. Bivalves, especially *Similodonta* sp., are common and include *Nuculites planulatus*, *Praeleda* sp., *Cuneamya* cf. *miamiensis* and *Modiolopsis* spp. A and B, many occurring for the first time. Gastropods are represented by *Kokenospira* sp., *Temnodiscus* sp., *Liospira* sp., *Cymbularia* sp. and *Carinaropsis* sp. and are never abundant but always persistent. The monoplacophoran *Archinacella* sp. makes its first appearance, as do the rare orthocones '*Orthoceras*' cf. *subundulatum*, '*O. pictum*', *Poterioceras* sp. and *Cyrtoceras* sp.

The uppermost faunal assemblage of the Acton Scott Formation of the Onny Valley is very distinct from the preceding unit. Not only is the total fauna less diverse and with a lower density, but there is also a significant species turnover event. The unit as a whole is characterized by

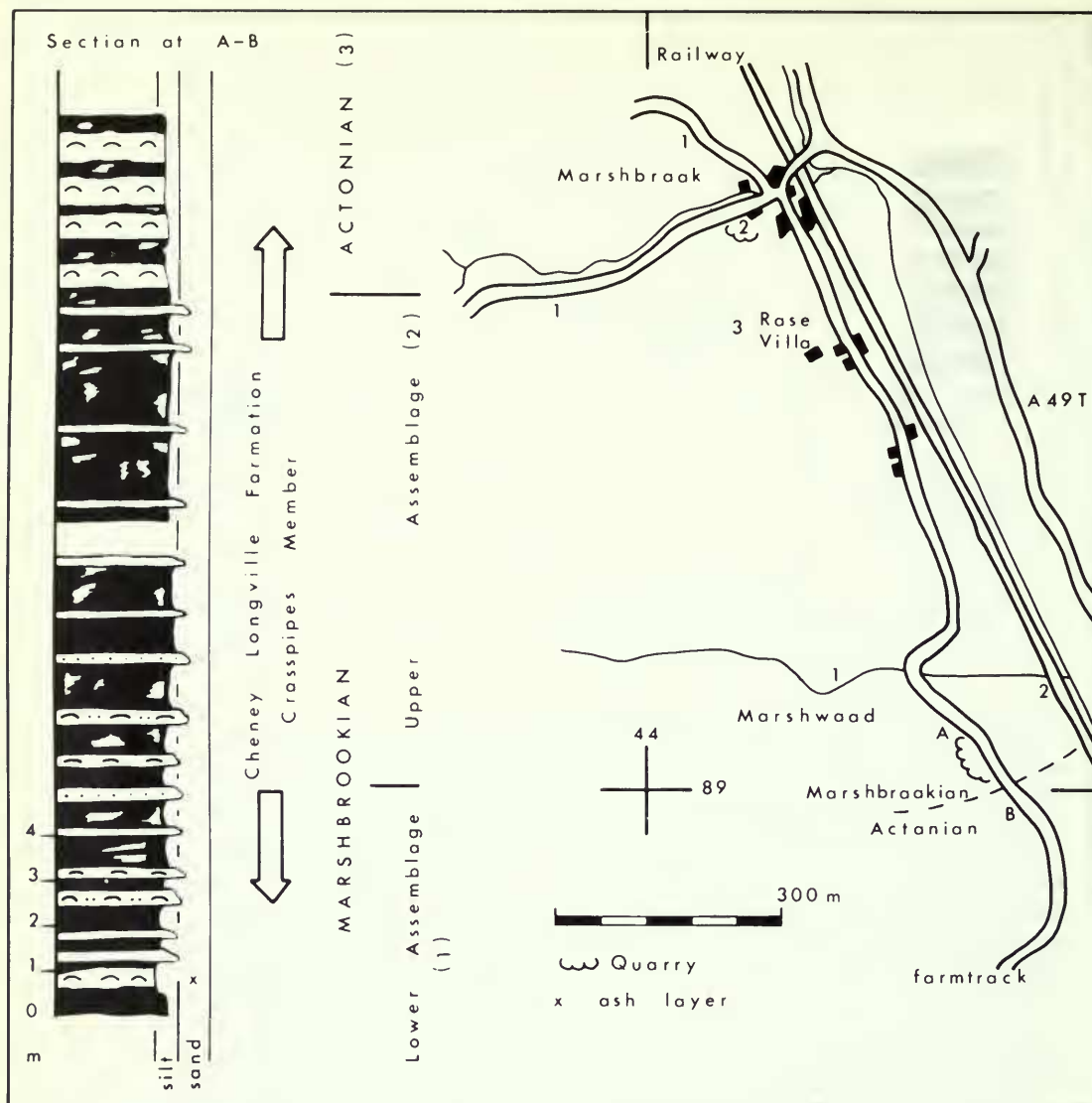


Fig. 14 Location and stratotype section for the boundary between the Marshbrookian and Actonian Stages. Symbols explained in Fig. 4.

diversity of trilobites such as *Ampyxella edgelli*, *Tretaspis ceriodes favus*, *Calyptaulax actonensis*, *Lonchodomas pennatus*, *Flexicalymene laticeps*, *Platylichas laxatus*, *Illaeus (Parillaenus) cf. fallax* and *Remopleurides latus onniensis*. However, the most abundant species are still brachiopods, particularly *Onniella depressa* (which replaces *O. reuschi*) and *Cryptothyris paracyclica*. *Eoplectodonta cf. rhombica* occurs persistently and for the first time, but is never common. Bryozoans are rare and limited to a single ramose form. Bivalves are still represented mainly by *Similodonta* sp. and subordinate *Nuculites planulatus*, but gastropods are rarer, chiefly *Kokenospira* and also *Lytospira* sp. and *Clathrospira* sp.

In the Acton Scott area there is a local variation in this assemblage. *Nicolella actoniae* is locally abundant in some limestone bands and *Cryptothyris paracyclica* is consistently more abundant than *Onniella depressa*. *Leptestiina oepiki* is more common and *Eoplectodonta cf. rhombica* is

Stage	Onny Valley	Marshbrook	Soudley	Chatwall (Dean 1960)	Chatwall (this paper)
Woolstonian	Glynbara Member	G. M.	G. M.	Cheney Langville Flags	Glynbara Member
	ALTERNATA Limestone Formation	A. L. F.	A. L. F.	Alternata Limestone ?	? — ? Chatwall Limestone Formation
Longvillian	U Harderley	M ? H.	H. S. F.	Chatwall Sandstone	Chatwall Sandstone Formation
	M Sandstone				? — ? Chatwall
Soudleyan	L Formation	L F.		Chatwall Flags	Flags

Fig. 15 Correlation problems and possibilities at the base of the Alternata Limestone Formation and between the middle Caradoc strata of the Soudley - Onny Valley and Chatwall districts.

absent. These changes correlate with a change in sediment grain size from calcareous silty muds to calcareous sandy silts.

The Onny Shale Formation has been divided into three successive trilobite zones (Bancroft 1929b): *Onnia cobboldi*, *O. gracilis* and *O. superba*. Two assemblages are recognized here, one which corresponds to the two lower zones and one to the upper zone.

The basal faunal assemblage is not diverse but abundant and characterized by large numbers of well-preserved *Onnia*. Other trilobites include *Calyptaulax actoniensis*, *Chasmops extensus*, *Iliaenus* (*Parillaenus*) cf. *fallax*, *Lonchodomas pennatus*, *Flexicalymene onniensis*, *Platylchas laxatus*, *Remopleurella burmeisteri* and *Tretaspis ceriodes favus*. Many of these occur in the preceding assemblage, but the rare *C. actoniensis*, *C. extensus* and *P. laxatus* only occur in the lower part of the assemblage. Brachiopods are abundant but not diverse. There is a sudden introduction of large *Onniella broeggeri* (which replaces *O. depressa*) and also *Sericoidea homolensis*, both of which may dominate horizons. Other brachiopods are rare, but include the first occurrence of *Christiania hollii*. Harper (1978) has recorded a rare assemblage with *Heterorthis alternata*, *Onniella* and *Sowerbyella*. Bivalves are not diverse but they are often abundant and are dominated by palaeotaxodonts such as *Nuculites planulatus*, with subordinate *Palaeonucula* sp., *Modiolopsis* sp. B and *Similodonta* sp. Gastropods, though rare, commonly include *Cymbularia* sp., *Sinuities* sp., *Lytospira* sp. and *Temnodiscus* sp.

The uppermost assemblage of the Onny Shale is characterized by its depauperate fauna. Very small *Onniella* sp. (*O. broeggeri* ?) and *Sericoidea* sp. (*S. homolensis* ?) occur, but specific identification is impossible because they are so immature (c. 2 mm wide). However, *Christiania hollii* increases in abundance from the underlying faunal assemblage, and *Schizocrania hewardi* appears; both are small forms. The trilobites are reduced in numbers, the most common being *Onnia superba*, but also *Triarthrus* cf. *linnarssoni*, *Pseudosphaerexochus* sp. and *Eobronteus* sp. *Ampyxella edgelli*, *Lonchodomas pennatus* and *Remopleurella burmeisteri* carry over from the preceding assemblage but are very rare.

Harper (1978) has described a thin discontinuous layer of *Heterorthis alternata* in a fine sandstone matrix of the distal bioturbated muds in the uppermost beds of the type Onnian. Other notable faunal elements include *Onniella* and *Sowerbyella*. It is probable that at least *H. alternata* and *Sowerbyella* were introduced by the distal effects of a storm pulse from a near-shore environment (Hurst 1979). As the *Onniella* was not specifically determined it is not known whether it was

significantly transported (cf. Hurst 1978). This find demonstrates that *H. alternata* is not a good stratigraphic indicator for the Woolstonian. But this unusual occurrence may have palaeogeographic implications; *H. alternata* is common in near-shore environments and its presence in the Onnian suggests their encroachment and may possibly indicate the persistence of the feature responsible for the Henley Member into Onnian times. Alternatively, the Henley Member may be a correlative of the Onnian Onny Shale Formation.

Outside the Onny Valley, the Henley Member contains a mixture of faunas but it is difficult to assess their spatial and temporal ranges, owing to the poor exposures, but in the quarry at SO 449896 two faunal assemblages occur (Fig. 9). The lower one is a low diversity and density assemblage dominated by abundant, but small, *Dalmanella unguis ultima*, less common *Strophomena grandis* and rare *Hedstroemina fragilis*, *Reuschella bilobata* and *Leptestiina* sp. The most abundant species is *Tentaculites anglicus*, whilst a prasopodid bryozoan is also common, as is the trilobite *Broeggerolithus transiens*, but only two other rare species have been recorded, *Primaspis caractaci* and *Gravicalymene* cf. *praecox*. This assemblage is similar in species content to the middle faunal unit of the Crosspipes Member.

Above comes a more diverse and altogether richer faunal assemblage (Fig. 9) dominated by *Onniella reuschi* and *Sowerbyella sericea*. *Hedstroemina fragilis* and *Kjerulfina polycyma* are also abundant in certain beds. Other diagnostic but less common species include *Rhactorthis actoniae*, *Leptaena salopiensis* and *Obolus* sp. *Tentaculites anglicus* is rare, whilst bryozoan diversity increases to include ramose, stick and prasopodid morphotypes. The trilobite fauna is not diverse nor common and only two species, *Broeggerolithus transiens* and *Gravicalymene* cf. *praecox*, have been found. This assemblage also parallels the uppermost faunal unit of the Crosspipes Member.

The small isolated rock garden exposure at Acton Scott (SO 454893) contains an assemblage unique in the whole of the type upper Caradoc succession, dominated by *Cryptothyris paracyclica* and *Dalmanella unguis ultima* with subordinate *Skenidioides* cf. *costatus*, *Leptestiina* sp., *Paracraniops doyleae*, *Orbiculoidea salopiensis* and *Dolerorthis virgata*. Trilobites are rare and include *Gravicalymene* cf. *praecox*, *Primaspis caractaci* and *Otarion* sp. Ramose bryozoan colonies are common.

The type section for the Chatwall Sandstone and Chatwall Limestone Formations is now conserved and thus no faunal collecting was possible from there. However, the Chatwall Sandstone Formation contains little fauna: Dean (1960a) reported rare *Kjaerina* aff. *jonesi*, *Sinuities* sp. and *Lophospira* cf. *gyrogonia* in the lower half, and at the very top *Dalmanella lepta*, *Rostricellula* sp., *Sowerbyella soudleyensis*, *Broeggerolithus* cf. *globiceps*, *Brongniartella* cf. *parva*, ? *Parabasilius powisii* and *Lophospira* sp. ind. The assemblage from the Chatwall Limestone Formation (see also list in Dean 1960a) is similar to that found in the uppermost Horderley Sandstone Formation, Alternata Limestone Formation and overlying lowermost Cheney Longville Formation of the Onny Valley.

Chronostratigraphy: Stage definitions and recognition

When Bancroft (1929a, b, 1933, 1945) erected the Caradoc Stages he defined them by means of brachiopods and trilobites (see Fig. 3, p. 189) but, although Bancroft gave type areas for the stages, he did not tie the boundaries down in particular sections. This fault is remedied here. All stages are defined within the southern area, between Acton Scott and Cheney Longville, as indicated by Bancroft and where possible in the Onny Valley itself.

a. Woolstonian Stage

Previously termed the Upper Longvillian Substage, the new name (after the village of Woolston, SO 424872, two miles north of the Onny Valley) is introduced for several reasons. The original concept of a Longvillian Stage (Bancroft 1929a) encompasses a great deal of strata within which there is a bipartite faunal division. In the type area the Upper Substage (= Woolstonian) is characterized by a sudden influx of *Heterorthis alternata*, *Trematis punctata*, *Broeggerolithus longiceps* and *Brongniartella bisulcata*. Bancroft (1929a) stated that the Longvillian Stage was

Table (cont.)

	ALF	CLF					ASF		OSF	
		GM		CM			RM	WM		
		1	2	1	2	3			1	2
<i>Nicolella actoniae</i> (J. de C. Sowerby, 1839)	-	-	-	-	-	-	R	R	-	-
<i>Obolus salopiensis</i> sp. nov. (p. 223)	-	-	-	-	-	-	R	R	R	-
<i>Onniella broeggeri</i> Bancroft, 1928	-	-	-	-	-	-	-	-	C	P
<i>Onniella depressa</i> Bancroft, 1945	-	-	-	-	-	-	-	C	-	-
<i>Onniella reuschi</i> Bancroft, 1928	-	-	-	-	-	VC	C	-	-	-
<i>Orbiculoidea ovata</i> sp. nov. (p. 230)	-	-	-	-	-	-	R	-	-	-
<i>Orbiculoidea</i> sp.	-	-	-	-	-	-	-	R	-	-
<i>Palaeoglossa lockleyi</i> sp. nov. (p. 225)	-	-	-	R	R	R	R	-	-	-
<i>Paracraniops doyleae</i> sp. nov. (p. 227)	R	R	R	R	R	R	R	-	-	-
<i>Paterula</i> cf. <i>subcircularis</i> Cooper, 1956	-	-	-	-	-	-	-	-	R	-
<i>Paterula</i> sp.	-	-	-	-	-	-	R	-	-	-
<i>Platystrophia</i> sp. 1	-	-	-	-	R	-	-	-	-	-
<i>Platystrophia</i> sp. 2	-	-	-	-	-	-	R	-	-	-
<i>Plectorthid</i> gen. et sp. indet.	-	-	-	-	-	-	R	-	-	-
<i>Pseudolingula</i> sp.	-	-	-	-	-	R	R	-	-	-
<i>Reuschella bilobata</i> (J. de C. Sowerby, 1839)	R	R	R	R	R	R	R	R	-	-
<i>Rhactorthis</i> cf. <i>crassa</i> Williams, 1963	-	-	-	-	-	-	R	-	-	-
<i>Rhactorthis grandis</i> sp. nov. (p. 239)	-	-	-	-	-	R	-	-	-	-
<i>Schizocrania hewardi</i> sp. nov. (p. 229)	-	-	-	-	-	-	-	-	-	C
<i>Schizocrania salopiensis</i> Williams, 1974	-	-	-	-	R	R	R	-	-	-
<i>Schizotreta</i> sp. 1	-	-	-	-	-	-	-	-	-	R
<i>Schizotreta</i> sp. 2	-	-	-	-	-	-	R	-	-	-
<i>Sericoidea homolensis</i> Havlíček, 1967	-	-	-	-	-	-	-	-	C	C
<i>Skenidioides</i> cf. <i>costatus</i> Cooper, 1956	-	-	-	-	-	-	R	-	-	-
<i>Sowerbyella sericea</i> (J. de C. Sowerby, 1839)	VC	P	R	C	R	C	R	-	-	-
<i>Strophomena grandis</i> (J. de C. Sowerby, 1839)	-	-	-	R	R	-	-	-	-	-
<i>Trematis punctata</i> (J. de C. Sowerby, 1839)	R	-	-	-	-	-	-	-	-	-
<i>Triplexia</i> sp.	-	-	-	-	-	-	R	-	-	-
? <i>Zygospira</i> sp.	-	-	-	-	-	-	R	-	-	-
BRYOZOA										
prasoporiid morphotype	R	R	R	P	R	R	R	-	-	-
ramose morphotype	R	R	R	R	R	R	R	-	-	-
stick morphotype	R	R	R	R	R	R	R	-	-	-
BIVALVIA										
? <i>Ambonychia radiata</i> Hall, 1847	-	R	R	-	-	-	-	-	-	-
? <i>Avicula orbicularis</i> Hall, 1843	R	R	R	R	R	R	R	R	-	-
<i>Cuneamya</i> cf. <i>miamiensis</i> Hall & Whitfield, 1875	-	-	-	-	-	-	R	-	-	-
<i>Cyclochoncha</i> sp.	-	-	-	-	-	-	R	-	-	-
? cyclochonchid	-	-	-	-	-	-	R	-	-	-
? <i>Modiolodon</i> sp.	R	-	-	-	-	-	-	-	-	-
<i>Modiolopsis</i> sp. A	-	-	-	R	R	R	R	R	-	-
<i>Modiolopsis</i> sp. B	-	-	-	-	-	-	R	R	-	-
<i>Modiolopsis</i> sp.	-	-	-	-	-	-	R	-	-	-
<i>Modiolopsis</i> cf. <i>modiolaris</i> (Conrad, 1838)	R	R	R	-	-	-	-	-	-	-
Modiolopsidae	-	-	-	R	R	R	-	-	-	-
<i>Nuculites planulatus</i> Conrad, 1841	-	-	-	R	R	R	R	P	R	R
? <i>Nuculites</i> sp.	-	-	-	-	-	-	-	-	R	-
<i>Palaeoneilo</i> sp.	-	-	-	R	R	R	R	-	-	-
<i>Palaeonucula</i> sp.	-	-	-	-	-	-	R	R	R	-

Table (cont.)

	ALF	CLF					ASF		OSF	
		GM		CM			RM	WM	1	2
		1	2	1	2	3				
? <i>Praearca</i> sp.	—	—	—	—	—	—	R	R	—	—
? <i>Praeleda</i> sp.	—	—	—	—	—	—	R	R	—	—
<i>Similodonta</i> sp.	—	R	R	R	R	R	P	P	R	R
undetermined bivalves	R	R	R	R	R	R	R	R	R	R
CEPHALOPODA										
? <i>Cyrtoceras</i> sp.	—	—	—	—	R	—	—	—	—	—
? <i>Orthoceras</i> <i>pictum</i> Blake, 1882	—	—	—	—	—	—	R	R	—	—
? <i>Orthoceras</i> cf. <i>subundulatum</i> Portlock, 1843	—	—	—	—	—	—	R	R	—	—
? <i>Poterioceras</i> sp.	—	—	—	—	—	—	R	—	—	—
GASTROPODA										
? <i>Arjamannia</i> sp.	—	—	—	—	—	—	—	R	—	—
<i>Carinaropsis</i> sp.	—	—	—	—	—	—	R	—	—	—
<i>Clathrospira</i> sp.	—	—	—	—	—	—	—	R	—	—
<i>Cymbularia</i> sp.	—	—	—	—	—	—	R	R	R	—
<i>Kokenospira</i> sp.	—	—	—	—	—	—	R	R	—	—
<i>Liospira</i> sp.	—	—	—	—	—	—	R	R	—	—
<i>Lophospira</i> sp.	—	—	—	—	R	R	—	—	—	—
<i>Lytospira</i> sp.	—	—	—	—	—	—	—	R	R	—
<i>Phragmolites</i> sp.	—	—	—	—	R	—	—	—	—	—
<i>Sinuities</i> sp.	—	—	—	—	—	R	R	R	R	—
<i>Temnodiscus</i> sp.	—	—	—	—	—	—	R	R	R	—
<i>Trochonema</i> sp.	—	—	—	—	R	—	—	—	—	—
indeterminate bellerophonaceans	—	—	—	—	—	—	R	R	R	—
indeterminate gastropod sp. 1	—	—	—	—	—	—	—	R	—	—
indeterminate gastropod sp. 2	—	—	—	—	—	—	—	R	—	—
indeterminate gastropods	R	R	R	R	R	R	R	R	R	—
indeterminate pleurotomariaceans	—	—	—	—	—	—	R	R	—	—
indeterminate trochiforms	R	—	—	—	—	—	R	—	—	—
MONOPLACOPHORA										
<i>Archinacella</i> sp.	—	—	—	—	—	—	R	R	—	—
<i>Cyrtolites</i> sp.	—	—	—	—	—	—	—	—	R	—
indeterminate monoplacophorans	—	—	—	—	—	—	R	R	R	—
OSTRACODA										
<i>Tallinnella scripta</i> (Harper, 1947)	R	R	R	R	R	R	R	—	—	—
<i>Primitia</i> sp.	—	—	—	—	—	R	R	R	R	R
TRILOBITA										
<i>Ampyxella edgelli</i> (Reed, 1910)	—	—	—	—	—	—	—	R	R	R
<i>Broeggerolithus longiceps</i> (Bancroft, 1929)	R	R	R	—	—	—	—	—	—	—
<i>Broeggerolithus transiens</i> (Bancroft, 1929)	—	—	R	R	R	R	—	—	—	—
<i>Brongniartella bisulcata</i> (M'Coy, 1851)	R	R	R	R	R	R	—	—	—	—
<i>Calypptaulax actonensis</i> Dean, 1961	—	—	—	—	—	—	R	R	R	—
<i>Chasmops extensus</i> (Boeck, 1837)	R	R	R	R	R	R	R	R	R	—
<i>Decoroproetus</i> sp.	—	—	—	—	R	—	—	—	—	—
<i>Encrinurus</i> sp.	—	—	—	—	R	—	—	—	—	—
? <i>Eobronteus</i> sp.	—	—	—	—	—	—	—	—	—	R
<i>Flexicalymene caractaci</i> (Salter, 1865)	—	—	—	R	R	R	—	—	—	—

Table (cont.)

	ALF	CLF					ASF		OSF	
		GM		CM			RM	WM		
		1	2	1	2	3				
<i>Flexicalymene cobboldi</i> Dean, 1962	R	R	R	-	-	-	-	-	-	-
<i>Flexicalymene laticeps</i> (Bancroft, 1949)	-	-	-	-	-	-	R	R	-	-
<i>Flexicalymene onniensis</i> (Shirley, 1936)	-	-	-	-	-	-	-	-	R	R
<i>Flexicalymene salteri</i> (Bancroft, 1949)	-	-	-	-	-	-	-	R	-	-
<i>Gravicalymene inflata</i> Dean, 1962	-	-	-	-	-	-	-	-	R	-
<i>Gravicalymene</i> cf. <i>praecox</i> (Bancroft, 1949)	-	-	-	-	-	-	-	-	R	-
<i>Illaenus</i> cf. <i>fallax</i> Holm, 1882	-	-	-	-	-	-	-	-	R	-
<i>Illaenus</i> sp.	-	-	-	-	-	-	-	R	R	-
<i>Kloucekia</i> (<i>Phacopidina</i>) <i>apiculata</i> (M'Coy, 1851)	R	R	R	-	-	-	-	-	-	-
<i>Lonchodomas pennatus</i> (La Touche, 1884)	-	-	-	-	-	-	-	R	R	R
<i>Onnia cobboldi</i> (Bancroft, 1929)	-	-	-	-	-	-	-	-	P	-
<i>Onnia gracilis</i> (Bancroft, 1929)	-	-	-	-	-	-	-	-	C	-
<i>Onnia superba</i> (Bancroft, 1929)	-	-	-	-	-	-	-	-	-	C
<i>Otarion</i> sp.	-	-	-	R	R	R	-	-	-	-
<i>Platylchas laxatus</i> (M'Coy, 1846)	-	-	-	-	-	-	-	R	R	-
<i>Primaspis caractaci</i> (Salter, 1853)	-	-	-	-	-	R	R	-	-	-
<i>Pseudosphaerexochus</i> sp.	-	-	-	-	-	-	-	-	-	R
<i>Remopleurella burmeisteri</i> (Bancroft, 1949)	-	-	-	-	-	-	-	-	R	R
<i>Remopleurides latus onniensis</i> Dean, 1962	-	-	-	-	-	-	-	R	-	-
<i>Tretaspis ceriodes favus</i> Dean, 1963	-	-	-	-	-	-	-	R	R	-
<i>Triarthrus</i> cf. <i>linnarssoni</i> Thorslund, 1940	-	-	-	-	-	-	-	-	-	R

MISCELLANEA

<i>Hyolithes</i> sp.	-	-	-	-	-	-	-	-	-	R
solitary corals	-	-	-	-	-	-	-	R	-	-
crinoid ossicles	R	R	R	R	R	R	R	-	-	-
phyllocariids	-	-	-	-	-	-	-	-	R	R

The junction between the Horderley Sandstone Formation and Alternata Limestone Formation is seen in the bed of the Onny River (SO 418856). This is the standard section for the base of the Woolstonian Stage and is shown in Fig. 12. The base of the Woolstonian coincides with the base of the Alternata Limestone Formation. The topmost collection from the Horderley Sandstone Formation (Hurst 1979) contained small *Kjaerina bipartita* (61%), *Sowerbyella sericea* (21%), small *Bancroftina typa* (4%), *Brongniartella minor* (2%), ramose bryozoan (2%), prasopodid bryozoan (10%) and rare round crinoid ossicles. The lowermost Alternata Limestone Formation collection contained large *Bancroftina typa* (53%), *Sowerbyella sericea* (23%), *Heterorthis alternata* (15%), *Trematis punctata* (7%), *Brongniartella bisulcata* (2%) and fragments of gastropods. Some 5 cm above this collection the fauna contained in a single bed included *Trematis punctata* (11%), large *Bancroftina typa* (13%), *Heterorthis alternata* (65%), large *Kjaerina bipartita* (5%), *Sowerbyella sericea* (1%), *Broeggerolithus longiceps* (2%), *Modiolopsis* cf. *modiolaris* (2%) and an indeterminate trochid gastropod (1%). The sudden influx of *H. alternata* and *T. punctata* marks the base of the Woolstonian.

Bancroft (1945 : 183) stated that the type section for the Upper Longvillian was 'in the Longville Flags of Longville Lane, from the base of the Alternata Limestone to the Earthwork'. Most of the lower part of this section is now overgrown, but the upper part is exposed and includes the type section for the Woolstonian/Marshbrookian boundary.

The junction between the Glynboro Member and the Crosspipes Member of the Cheney Longville Formation is seen in the roadside at SO 418851, and that section forms the standard for the

Woolstonian/Marshbrookian boundary (Fig. 13). The uppermost single bed collection in the Woolstonian contains *Dalmanella multiplicata multiplicata* (40%), *Kjaerina typa* (18%), *Tentaculites anglicus* (20%), *Paracraniops doyleae* (2%), *Broeggerolithus longiceps* (2%), *Flexicalymene caractaci* (2%), prasopodid bryozoan (6%), ramose bryozoan (10%) and round crinoid ossicles. Some 110 cm of strata follows in which a non-diagnostic fauna occurs (Fig. 13). This includes *Dalmanella multiplicata multiplicata* (37%), *Bancroftina hewitti* (7%), *Kjaerina typa* (3%), *Tentaculites anglicus* (23%), *Paracraniops doyleae* (13%), *Broeggerolithus longiceps* (3%), *Brongniartella bisulcata* (3%), prasopodid bryozoans (7%) and ramose bryozoans (3%). Some 30 cm above the last collection a diagnostic lower faunal assemblage of the Marshbrookian appears, containing *Dalmanella multiplicata multiplicata* (33%), *Bancroftina hewitti* (1%), *Kjerulfina trigonalis* (2%), *Strophomena grandis* (2%), *Sowerbyella sericea* (15%), *Broeggerolithus transiens* (1%), *Flexicalymene caractaci* (1%), *Brongniartella bisulcata* (1%), *Tentaculites anglicus* (16%), prasopodid bryozoan (26%), ramose bryozoans (1%), smooth and ribbed ostracods, and round and pentagonal crinoid ossicles. The loss of *K. typa* and the introduction of a more diverse fauna with *S. sericea*, *K. trigonalis*, *S. grandis*, *B. hewitti* and *B. transiens* marks the boundary between the two stages.

b. Marshbrookian Stage

Bancroft (1945 : 183) stated that the type section for this unit was through 'the highest beds of the Longville Flags as exhibited in the lane through Marsh Wood'. This is still the best section (SO 445890), even though it is now becoming overgrown, but unfortunately the base of the Marshbrookian is not exposed (see Fig. 14). The top of the uppermost faunal assemblage of the Crosspipes Member (*Onniella reuschi* Zone of Bancroft) has always been taken as the boundary between the Marshbrookian and Actonian. However, this boundary is here redefined to coincide with the top of the middle assemblage (*Dalmanella unguis* Zone of Bancroft) of the Crosspipes Member. The stratotype is defined in the cart track just to the south of Marshwood Quarry (Fig. 14).

The Marshbrookian/Actonian boundary is redefined here, because a major faunal turnover and species replacement, with a major change in diversity and density, occur at this point, i.e. between the middle and upper faunal assemblages of the Crosspipes Member of the Cheney Longville Formation. The boundary is traceable throughout the Caradoc district and in fact was partially exposed through trenching in the Onny Valley (SO 422854; see Fig. 8); it is accessible in the stream section at Ragleth Hill (SO 451908 to SO 451906; see Fig. 7). Such redefinition limits the diverse *Onniella* faunas of the Upper Caradoc to post-Marshbrookian strata and the majority of the less diverse *Dalmanella*-dominated faunas to the pre-Actonian.

In the standard section for the boundary (Fig. 15) the uppermost single bed collection from the Marshbrookian contains the following species: *Dalmanella unguis unguis* (20%), *Paracraniops doyleae* (7%), *Hedstroemina fragilis* (3%), *Sowerbyella sericea* (3%), *Strophomena grandis* (3%), *Chonetoida radiatula* (1%), *Tentaculites anglicus* (49%), *Broeggerolithus transiens* (2%), *Flexicalymene caractaci* (1%), *Brongniartella bisulcata* (1%), *Decoroproetus* sp. (1%), *Otarion* sp. (1%), prasopodid bryozoans (7%), thin ramose bryozoans (1%), smooth and ribbed ostracods and round and pentagonal crinoid ossicles. Precisely 1 m higher stratigraphically, the lowest collection from the Actonian contains *Onniella reuschi* (59%), *Sowerbyella sericea* (8%), *Hedstroemina fragilis* (5%), *Kjerulfina polycyma* (1%), *Palaeoglossa lockleyi* (0.5%), *Paracraniops doyleae* (0.5%), *Schizocrania salopiensis* (0.5%), *Reuschella bilobata* (1.5%), *Heterorthis alternata* (0.5%), *Rhactorthis grandis* (1%), *Similodonta* sp. (5%), *Modiolopsis* sp. A (3%), '*Avicula*' cf. *orbicularis* (3%), *Nuculites planulatus* (3%), *Flexicalymene caractaci* (1%), *Primaspis caractaci* (0.5%), *Tentaculites anglicus* (4%), prasopodid bryozoans (2%), ramose bryozoans (2%), indeterminate gastropods (1%) and some round crinoid ossicles.

This abrupt faunal change is one of the most prominent in the upper Caradoc sequence and may represent more than just a local ecological event.

c. Actonian Stage

Bancroft (1945 : 183) listed the type locality for the Actonian as 'the Acton Scott Beds below the

Onnia horizon in the Onny River section east of Burrell's Coppice'. This is the only possible locality for a more or less uninterrupted section, albeit largely unexposed, of this stage (Fig. 8). The base of the Actonian as understood here, or indeed as Bancroft defined it, is not exposed (SO 422854), thus the lower boundary is placed at the locality for the type Marshbrookian (Fig. 14).

d. Onnian Stage

The Onnian is defined, following Bancroft, in the Onny Valley river section between SO 425854 and SO 426854. Bancroft defined the base of the stage, and thus the top of the Actonian, by the sudden appearance of the trilobite genus *Onnia*. There is no need to alter this definition of the Actonian–Onnian stratotype, which is only partially exposed at one locality in the river bed, at SO 425854 (Fig. 8). The boundary is recognizable by the introduction of several new genera and species, not just *Onnia*. The highest single bed collection in the Actonian yielded *Onniella depressa* (14%), *Cryptothyris paracyclia* (2%), *Dolerorthis virgata* (2%), *Eoplectodonta* cf. *rhombica* (25%), *Obolus salopiensis* (3%), *Similodonta* sp. (9%), *Nuculites planulatus* (3%), *Palaeonucula* sp. (4%), *Praearca* sp. (9%), ? cyclonchiid (2%), indeterminate bivalves (5%), *Chasmops extensus* (1%), *Lonchodomas pennatus* (1%), *Ampyxella edgelli* (1%), *Remopleurides latus onniensis* (2%), *Flexicalymene laticeps* (1%), *Kokenospira* sp. (8%), *Cymbularia* sp. (2%), indeterminate gastropods (2%), 'Orthoceras' cf. *subundulatum* (1%), ramose bryozoans (1%), button bryozoans (1%) and smooth ostracods. A gap of 2–3 m intervenes before the lowest single Onnian collection which yielded *Onniella broeggeri* (44%), *Sericoidea homolensis* (20%), *Eoplectodonta* cf. *rhombica* (2%), *Paterula* cf. *subcircularis* (2%), *Onnia cobboldi* (10%), *Lonchodomas pennatus* (3%), *Chasmops extensus* (1%), *Gravicalymene* cf. *praecox* (4%), *Temnodiscus* sp. (2%), 'Orthoceras' cf. *subundulatum* (1%), *Nuculites planulatus* (9%), *Palaeonucula* sp. (1%) and smooth ostracods.

Correlation problems within the area

The Onny Valley is the only locality where the upper Caradoc formations are exposed in a more or less continuous sequence and uninterrupted by faulting. The sequence is also complete; that is, apart from the possible condensed sequence or non-sequence at the base of the Alternata Limestone Formation, there are no apparent stratigraphic breaks. However, in the Marshbrook to Soudley district there is certainly a non-sequence between the Alternata Limestone Formation and the underlying Horderley Sandstone Formation. Other problems are the correlation of the

Fig. 16 Soudley Quarry, SO 477918, showing the conformable contact (dotted line) between the Horderley Sandstone Formation (HS) and the Alternata Limestone Formation (AL). The whole of the Longvillian Stage is missing at the dotted line. Note that the Horderley Sandstone Formation is laminated sand whilst the Alternata Limestone Formation is an alternation of laminated sand and bioturbated sandy silts. Section height 2 m.

Fig. 17 Glynboro Member of the Cheney Longville Formation at the old river cliff locality in the Onny Valley at SO 422890. Note the alternation of thick laminated sand units (base of major sandstones marked by dotted line) and bioturbated sandy silts. Upper faunal assemblage; knife 25 cm.

Fig. 18 Swell lag shell layers in completely bioturbated sandy silts of the uppermost part of the Crosspipes Member of the Cheney Longville Formation at the Ragleth Hill stream section at SO 451908. Upper faunal assemblage, $\times 1$, BB 73673.

Fig. 19 A cross-bedded unit in the lower part of the Horderley Sandstone Formation in the Onny Valley at SO 4161 8578.

Fig. 20 Close-up of the basal Crosspipes Member of the Cheney Longville Formation at SO 419849. This is the basal faunal assemblage of the Marshbrookian. Note thicker bioturbated horizons than in the Glynboro Member. Knife 25 cm.

Fig. 21 Laminated and low-angled bedding (picked out by dotted shell beds) in the upper part of the Horderley Sandstone Formation in the Onny Valley at SO 4154 8593.

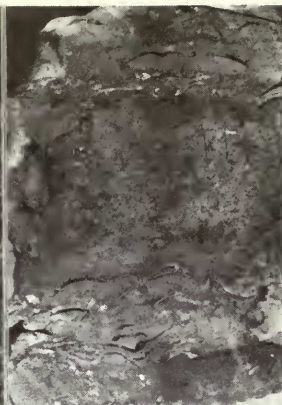
Fig. 22 Close-up of the Alternata Limestone Formation at Soudley Quarry, SO 477918. Knife 25 cm.



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Chatwall Sandstone Formation and Chatwall Limestone Formation with the sequence in the southern area, and the Henley Member of the Acton Scott Formation and its equivalent in the Onny Valley.

a. Base of the Alternata Limestone Formation

In the southern area Bancroft (1929a) indicated a stratigraphical break at the base of the Alternata Limestone Formation when he showed that at Soudley it rested on an Upper Soudleyan horizon in the Horderley Sandstone Formation (Fig. 15). Diggins (in discussion to Bassett *et al.* 1966) suggested that a break may occur throughout the Soudley/Cheney Longville area, at the base of the Alternata Limestone Formation, since he had found there phosphatic nodules, set in a yellow sandy limestone, in the basal 1 m. Re-examination of all the available sections confirms this observation. A further problem concerns the upper Horderley Sandstone Formation. In the area of the Onny Valley, the top 15 m contains the *Bancroftina typa* Zone of Bancroft (1933), but at Marshbrook the Alternata Limestone Formation rests directly on Horderley Sandstone Formation containing the *Dalmanella lepta* and *D. indica* Zones of Bancroft (1933). At Soudley the whole of this sequence is missing (Fig. 15). Throughout the whole area the basal part of the Alternata Limestone Formation is condensed or a non-sequence. However, at Soudley phosphatic nodules occur throughout the Alternata Limestone Formation, indicating that there the whole sequence may be condensed.

Hurst (1979) attempts to put the facies and faunal distributions at this horizon into an environmental model. It is apparent that, with these stratigraphic breaks in the Horderley Sandstone Formation, the base of the Alternata Limestone Formation in the Marshbrook and Soudley area could be older than in the Onny Valley. The base at Marshbrook and Soudley may be correlative with the uppermost beds of the Horderley Sandstone Formation (*B. typa* Zone) of the Onny Valley. However, this is thought unlikely for several reasons. The introduction of a distinct fauna dominated by *Heterorthis alternata* and *Trematis punctata* is sudden and in such a localized area as Soudley and the Onny Valley seems more likely to be geologically synchronous. Perhaps the most important consideration is the incorporation of phosphatic nodules in the basal beds of the Alternata Limestone Formation which is probably related to a transgressive event (cf. Cooper 1977), resulting in lack of sediment input into the basin and consequent formation of a condensed sequence.

b. Top of the Alternata Limestone Formation

The thickness of this formation varies, so it is possible that the top is diachronous. At Soudley the formation is only 1.5 m thick and contains phosphatic nodules throughout, possibly because it is condensed and not a result of facies migration as suggested by Hurst (1979). The deposits of the Alternata Limestone Formation are unlike any others in the Caradoc, and possibly indicate an environment influenced by marine bars (Hurst 1979). Thus in such a small geographic area as

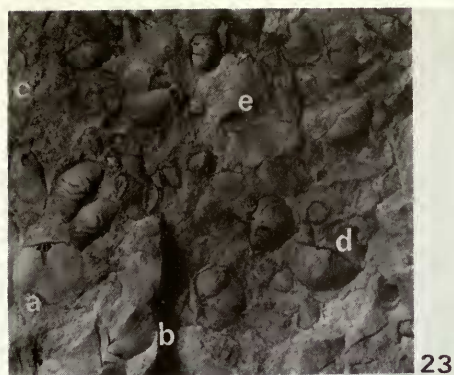
Fig. 23 Shell surface layer (swell lag) from the upper faunal assemblage of the Henley Member of the Acton Scott Formation at SO 449896. a = *Onniella reuschi* b.v., b = *O. reuschi* p.v., c = *Rhactorthis actoniae* b.v., d = *Sowerbyella sericea* p.v. and e = *S. sericea* b.v. $\times 0.6$, BB 73670.

Fig. 24 Shell lag layer from the Alternata Limestone Formation of Soudley Quarry at SO 477918. a = *Heterorthis alternata* p.v., b = *Kjaerina bipartita* p.v., c = *K. bipartita* b.v., d = *Sowerbyella sericea* p.v. and e = *S. sericea*. $\times 1.2$, BB 73668.

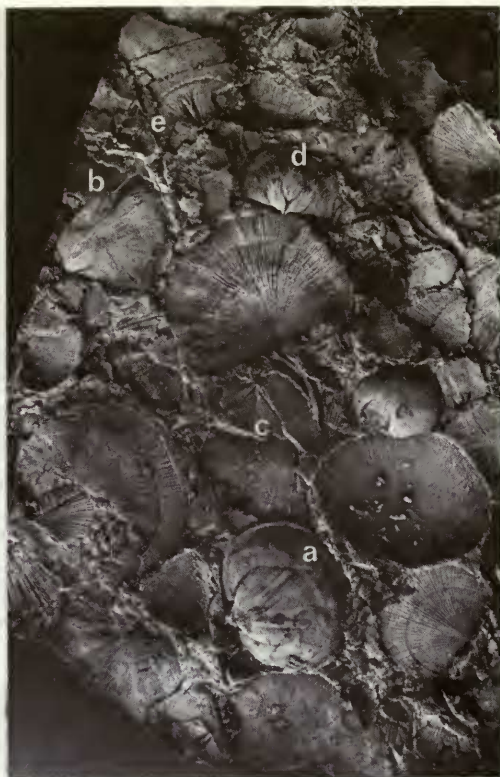
Fig. 25 Swell lag from the upper part of the middle faunal assemblage of the Crosspipes Member of the Cheney Longville Formation at Marshwood Quarry, SO 445890 (upper Marshbrookian faunal assemblage). a = *Dalmanella watti* p.v., b = *D. watti* b.v., c = *Strophomena grandis* p.v., d = praeopodid bryozoan, e = *Tentaculites anglicus*, f = *Brongniartella bisulcata* and g = *Flexicalymene caractaci*. $\times 1.5$, BB 73671.

Fig. 26 Swell lag shell layer from the Ragdon Member of the Acton Scott Formation at SO 451908. a = *Onniella reuschi* p.v., b = ? *Zygospira* sp. b.v., c = *Rhactorthis* cf. *crassa* b.v., d = *Nuculites planulatus*, e = *Similodonta* sp. $\times 1$, BB 73669.

All p.v. = internal moulds of pedicle valves; all b.v. = internal moulds of brachial valves.



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Soudley/Onny Valley, the passing of a peculiar sedimentary environment is likely to be geologically synchronous. However, the attenuated sequence at Soudley could be partly owing to a local facies disturbance such as the migration of marine bars (see Hurst 1979).

Thus it is not known whether the top of the Alternata Limestone Formation and the base of the overlying Cheney Longville Formation is synchronous or diachronous. At Soudley the top might be slightly older, but it is probably synchronous in the rest of the district.

c. Correlation with the Chatwall district

The correlation of the Chatwall Sandstone Formation and Chatwall Limestone Formation with the southern area is difficult. Dean (1960a) recognized two stratigraphical breaks in this district, bounding the Chatwall Sandstone Formation (his definition). However, Hurst (1979) has re-analysed these sequences and suggests that the breaks may not exist (see Fig. 15). The evidence for the breaks (Dean 1960a) was conglomerate horizons and missing faunal assemblages compared to the Onny Valley sequence. Viewed in the context of sedimentary sequences and environments there is nothing unusual about the conglomerate horizons. They are simply part of a laminated beach environment in which many pebble bed horizons occur (Hurst 1979). Consequently it is not surprising that faunal assemblages are also missing, as the marginal marine environments at Chatwall are different from the open marine equivalents in the Onny Valley.

Based on the evidence of transgressive events (derived from sedimentary criteria) in the Chatwall area, Hurst (1979) suggested that the base of the Chatwall Limestone Formation may correlate in part with the uppermost 15 m of the Horderley Sandstone Formation (*Bancroftina typa* Zone of Bancroft 1933; see Fig. 16). These sediments both indicate a slightly more offshore environment when compared to the immediately preceding strata. This transgressive pulse is the first to reverse the overall regressive nature of the sedimentation patterns in the Soudleyan–Lower

Fig. 27 *Brongniartella bisulcata*. Internal mould of cranidium, from the Cheney Longville Formation, Crosspipes Member, lowest faunal assemblage, near Cheney Longville. (In.52332, $\times 1.5$.)

Fig. 28 *Chasmops extensus*. Internal moulds of cranidia, from the Crosspipes Member (lower faunal assemblage) of the Cheney Longville Formation at Marsh Quarry, SO 445890. (In.50544, $\times 1.3$.)

Fig. 29 *Kloucekia (Phacopidina) apiculata*. Internal mould of cranidium, from the Alternata Limestone Formation in Cheney Longville Lane. (In.52157, $\times 2.3$.)

Fig. 30 *Broeggerolithus transiens*. Internal mould of cranidium, from same horizon and locality as Fig. 28. (In.50601, $\times 2$.)

Fig. 31 *Flexicalymene caractaci*. Internal mould of cranidium, from same locality as Fig. 28 but upper faunal assemblage of the Marshbrookian. (In.52230, $\times 1.5$.)

Fig. 32 *Remopleurella burmeisteri*. Internal mould of cranidium, from the Onny Shale Formation at SO 4258 8536. (In.51184, $\times 3$.)

Fig. 33 *Primaspis caractaci*. Cranidial plaster cast, from Ragdon Member of Acton Scott Formation at SO 4645 9013. (In.54907, $\times 2$.)

Fig. 34 *Lonchodomas pennatus*. Internal mould of cranidium, from same locality as Fig. 32. (In.37622, $\times 2.1$.)

Fig. 35 *Calyptaulax actonensis*. Cranidial plaster cast, from the Wistanstow Member of the Acton Scott Formation in the Onny Valley. (In.49773, $\times 2.5$.)

Fig. 36 *Onnia superba*. Internal mould of cranidium, from same locality as Fig. 32. (In.14674, $\times 2$.)

Fig. 37 *Onnia cobboldi*. Partially exfoliated cranidium, from Onny Shale Formation at SO 4257 8537. (In.50697, $\times 2$.)

Fig. 38 *Ampyxella edgelli*. Internal mould of cranidium; locality possibly the same as for Fig. 32. (In.48562, $\times 2$.)

Fig. 39 *Chasmops extensus*. Close-up of Fig. 28, $\times 1.6$.

Fig. 40 *Flexicalymene (Omnicalymene) laticeps*. Cranidium from the Wistanstow Member of the Acton Scott Formation in the Onny Valley. (In.50721, $\times 2.4$.)

Fig. 41 *Platylchus laxatus*. Internal mould of cranidium. Acton Scott Formation, Rose Villa, Marshbrook. (In.46446, $\times 1.6$.)

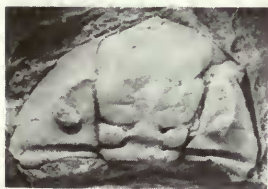
None of the figured trilobites are from the author's collections; some specimens are therefore not located precisely by grid references, as this information was not always available.



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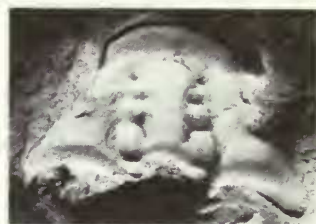
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Longvillian throughout the whole Caradoc area. The non-sequence at Marshbrook and the uppermost part of the one at Soudley, below the Alternata Limestone Formation, could be explained by this transgression (Fig. 15). The condensed sequence at the base of the Alternata Limestone Formation in the Soudley-Onny Valley region may also be a later pulse of the same transgression. If so, the second pulse had a greater effect and marks the beginning of the upper Caradoc transgression which continued to the deposition of the Onny Shale Formation.

Contrary to this, Dean (1958 : 216) argued that the fauna of *Heterorthis alternata*, *Sowerbyella sericea* and *Brongniartella bisulcata* makes it difficult to accept that the Chatwall Limestone Formation is of pre-Upper Longvillian (= Woolstonian) age. Such is not the case if it is accepted that many (if not all) species are facies-correlated, if not facies-controlled. An example of this is seen in the Actonian faunas in which the lowermost faunal assemblage of the Actonian reappears almost species for species with the same sedimentary facies in the upper Actonian Henley Member.

Nearshore sedimentary facies are ephemeral and it is likely that, whatever the relationship of the Alternata Limestone Formation to the Chatwall Limestone Formation, there is little time-difference to effect evolutionary faunal differences. It could be argued that this fauna represents a unique invasion and is likely to be geologically synchronous, but if two distinct transgressive pulses occurred in a short time (Hurst 1979) then two phases of the same faunal invasion could have taken place. Dean (1958, 1960a) also argued that the uppermost Chatwall Sandstone Formation had a great deal in common, sedimentologically, with the Chatwall Limestone Formation. Certainly the top 2–3 m of the Chatwall Sandstone Formation forms a sedimentological link with the overlying Chatwall Limestone Formation, but this is no reason to consider it of Woolstonian age or the base of the Chatwall Limestone Formation to be post-basal Woolstonian.

Thus it is considered unlikely that non-sequences occur in the exposed sections of the Chatwall Sandstone Formation. The sediments of the Upper Soudleyan and Lower Longvillian are indicative of a marginal marine environment, compared to the time-equivalents in the Onny Valley, and the attenuated nature of the Chatwall sequence may be simply a result of the differences in sedimentary regime, rather than non-sequences. The age of the base of the Chatwall Limestone Formation is equivocal. Dean (1958) considered that it may be slightly post-basal Upper Longvillian (= Woolstonian). However, his faunal and sedimentological evidence seems inadequate. Following the model proposed by Hurst (1979), it is suggested that the transgressive nature of the base of the Chatwall Limestone Formation correlates with a similar event in the top 15 m of the Horderley Sandstone Formation of the Onny Valley. If so, the top of the Chatwall Limestone Formation (which is not exposed) may be older than the top of the Alternata Limestone Formation and thus the base of the Cheney Longville Formation would be diachronous southwards (see Hurst 1979). This may explain why the Cheney Longville Formation is thickest in the Chatwall region (Greig *et al.* 1968), owing to its earlier initiation.

d. Acton Scott Formation

Following the deposition of the Alternata and Chatwall Limestone Formations, there is a transgression into the farthest-offshore Onny Shale Formation, and it seems probable that the bases of the members and formations are synchronous in such a small area. However, there is difficulty correlating the locally regressive Henley Member with the Onny Valley sequence in the Acton Scott Formation. Dean (1958 : 211) suggested that the stratigraphical position of the Henley Member, with a fauna of *Nicolella actoniae*, *Reuschella bilobata*, *Cryptothyris paracyclia*, *Leptaena*, *Platylichas*, *Chasmops*, *Primaspis* and *Gravicalymene*, supports a correlation with the lower part of the middle Actonian (= lower part of Wistanstow Member) of the Onny Valley. The fauna at the type section for the Henley Member is very similar to the lowest faunal assemblage of the Actonian, but this does not indicate that the Henley Member is lowermost Actonian, as it demonstrably occurs above that fauna in the Acton Scott area. It is arguable whether assemblage stratigraphy of this nature should be used even for local correlations.

Perhaps a more reliable way to attempt to correlate the Henley Member with the Onny sequence can be found by consideration of the sedimentary environments. The Henley Member is a highly

calcareous fine sandstone, whilst the Wistanstow Member is a calcareous siltstone. It is possible that the calcareous influx was synchronous. The base of the Henley Member is not exposed so that it is not possible to tie it precisely into the Onny Valley sequence, although it is unlikely to predate the Wistanstow Member, as at least 30 m of the Ragdon Member siltstone is known in the Acton Scott area.

The massive sandstones of the Henley Member are indicative of an environment shallower than the preceding Ragdon Member or the contemporaneous Wistanstow Member, and they suggest a swell or some submarine topographic feature in the Acton Scott area. The formation of such a sediment barrier in an open marine environment is associated with calcareous sediments and may be responsible for the calcareous siltstones of the Onny Valley (cf. Watkins 1979). Thus the removal of the feature would also affect carbonate sedimentation in the district. If such a model is correct then the Henley Member would equate with the whole of the Wistanstow Member of the Onny Valley. The basal Onny Shale Formation has only a small proportion of calcareous material in comparison with the underlying Wistanstow Member, indicating a change in sedimentary conditions such as the destruction of the conditions favourable to the formation of the Henley Member.

Correlation outside the Caradoc district

Within the type area there are many problems with correlation based on shelly faunas. Such faunas are facies-related, creating problems of accurate correlation between the remaining upper Caradoc sequences of the Anglo-Welsh area. Graptolites are of very limited use, not only because they are rare, but also because only two zones are now recognized in the upper Caradoc (Williams *et al.* 1972). Thus correlation with the type area must chiefly be by means of shelly faunas, mainly trilobites and brachiopods, but this creates problems. For instance, Cave (1965) recognized an Onnian fauna in an offshore mud environment in the Welsh Basin. The sedimentary environment is not precisely the same as the type Onnian, but it is very similar. But could this correlation have been effected if the environment happened to consist of nearshore sands, with a related fauna? Not all deposits of Onnian age will be found in offshore environments, but what does a nearshore Onnian fauna consist of?

Another difficulty is the Longvillian sediments of the Bala district in north Wales, which are predominantly muddy (Bassett *et al.* 1966), compared to the sandstones and siltstones of Caradoc. It is no wonder they found little in common for useful correlative purposes, but is the effected correlation correct? The species-similarity within facies may be misleading until more is known about phenotypic variation and ecological clinal variation (cf. Hurst 1978) of the groups involved.

Bancroft (1933) recognized upper Caradoc shelly faunas in the Cross Fell Inlier, which he equated with Longvillian through to the Ashgill. He recognized all the stages and attempted to recognize some of the south Salop zones, and this is the only other area in England or Wales where there is a possible occurrence of a complete upper Caradoc succession. However, in the light of the present work there is a need to revise the fauna completely and to study the sediments, not only to test the proposed correlations but also to ascertain if any stratigraphical breaks occur in the sequence.

Possibly the best marker horizon in the Caradoc is the non-sequence at the base of the Woolstonian. This probably resulted from the initiation of a transgression (Hurst 1979) which carried on into the Onnian. It is traceable into the Welsh Basin (Williams 1953; Cave 1965; Bassett *et al.* 1966) but based on conventional faunal correlations here the non- or condensed sequences last into the Marshbrookian, Actonian or even probably the Onnian. This transgression and production of non- or condensed sequences is obviously a regional event and could possibly prove to be the most widely correlatable horizon of the whole upper Caradoc sequence.

Correlation by means of ash falls is accurate but at the same time limited (Brenchley 1969). The only ash falls in the upper Caradoc are in the lowest faunal assemblage of the Marshbrookian, and there are at least three distinct events which can be pieced together from local sections. None of these ashes is reworked, for they occur in bioturbated beds, not associated with transported

sediment. There is no obvious correlative of these ash falls in the Welsh Basin, unless it is argued that the Longvillian ashes of the Bala district (Schiener 1970) are in fact Marshbrookian. When it is considered that the Bala area is correlated with the type section on faunas having very little in common it is difficult to be certain, but no ash falls have been located in any Longvillian or Woolstonian strata in the type Caradoc.

Recent conodont work (Bergström 1964) also highlights correlation problems in the Caradoc. For example, Bergström considered the south Wales Crûg Limestone to be of Marshbrookian age. Very little is known of type Marshbrookian conodonts, mainly owing to the clastic nature of the Caradoc facies. Thus conodont correlation with the type area must be indirect. Williams (1953 : 195) considered the Crûg Limestone to contain a Longvillian–Marshbrookian fauna, ‘probably equivalent to the Upper Longville Flags of the Welsh Borders’, whereas Williams *et al.* (1972) placed it in the Marshbrookian. The faunal list given by Williams (1953) shows little in common with the type Marshbrookian. Indeed the only species for correlation are the long-ranging *Sowerbyella sericea* and *Nicolella actoniae*, and *Kjaerina geniculata* which is restricted to the Woolstonian (= old Upper Longvillian). This emphasizes that with provincial micro- and macro-faunas (see Williams 1969*a, b*, 1972) there is considerable difficulty and ambiguity in correlating with the type sections (see also Dean 1960*c*).

The brachiopod faunas

The last systematic attempt to document type Caradoc brachiopods was undertaken by Bancroft (1928*a, b*, 1929*a*, 1933, 1945). Unfortunately, owing to many unhappy circumstances throughout his career, culminating in his premature death in the Second World War in 1944, he never achieved a complete revision of the whole brachiopod fauna. Thus in order to provide a sound basis for the ecological study of the upper Caradoc rocks it is of paramount importance that the taxonomy of this major invertebrate group is well documented.

Approximately 250 collections, numbering some 50,000 fossils, were made in 1974–76 and have been deposited in the British Museum (Natural History). Each collection is referred to by a code, e.g. WFT1, and allocated a locality number with a National Grid Reference. Many separate collections may come from a single locality. The registered numbers of the figured specimens lie within the ranges BB 72243 to BB 72543 and BB 73533 to BB 73646. Specimens in Birmingham University Museum are prefixed by the letters ST and those in the Geological Survey Museum by GSM. With the help of Dr L. R. M. Cocks, lectotypes have been chosen for all of Bancroft’s species; the ones not referred to in this study can be found in Cocks (1978). The data of bivariate statistics comprise over 100 tables and are too voluminous to publish; they have therefore been deposited in the Palaeontology Library of the British Museum (Natural History). However, they are to be regarded as an integral part of this study.

Systematic methods

The statistical methods adopted in this paper are those used by Williams (1962, 1963, 1974). Briefly, morphological variation displayed by conspecific specimens is quantified and then samples are tested against one another by standard statistical tests for significance.

Continuous variables are derived by measuring various standard components of the shell (Fig. 42). These are length of valve (l), width of valve (w), depth of valve (d), length of dorsal and ventral muscle scars (lsc), width of muscle scar (wsc), length of dental plates (dl), width of brachio-phore bases (wc) and length of septum (ls). Fig. 42 indicates where typical measurements were taken.

Such parameters are bivarately analysed by the reduced major axis method, to find correlations and express growth ratios. Differences in such parameters as growth ratios (a or α) are tested for significance. Continuous univariate characters, such as the wavelength of ribs at a given distance anteromedially of the umbo, are assumed to be normally distributed and compared by the t test. Discontinuous univariate characters, such as the relative branching of costellae enumerated

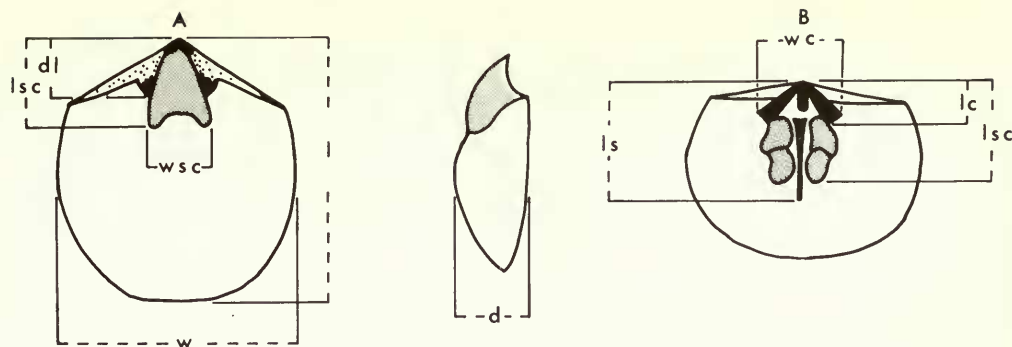


Fig. 42 Schematic representation of moulds of pedicle (A) and brachial (B) valves, showing measurements taken.

according to Bancroft's notation (Bancroft 1928a), have been compared by χ^2 tests, contingency, or 2×2 tables, depending on the sample size.

Generally if there are significant differences (at least at the 95% level) in two or more characters between two separate samples they are treated as belonging to two separate taxa.

All measurements given for length and width of figured material are in mm.

Localities

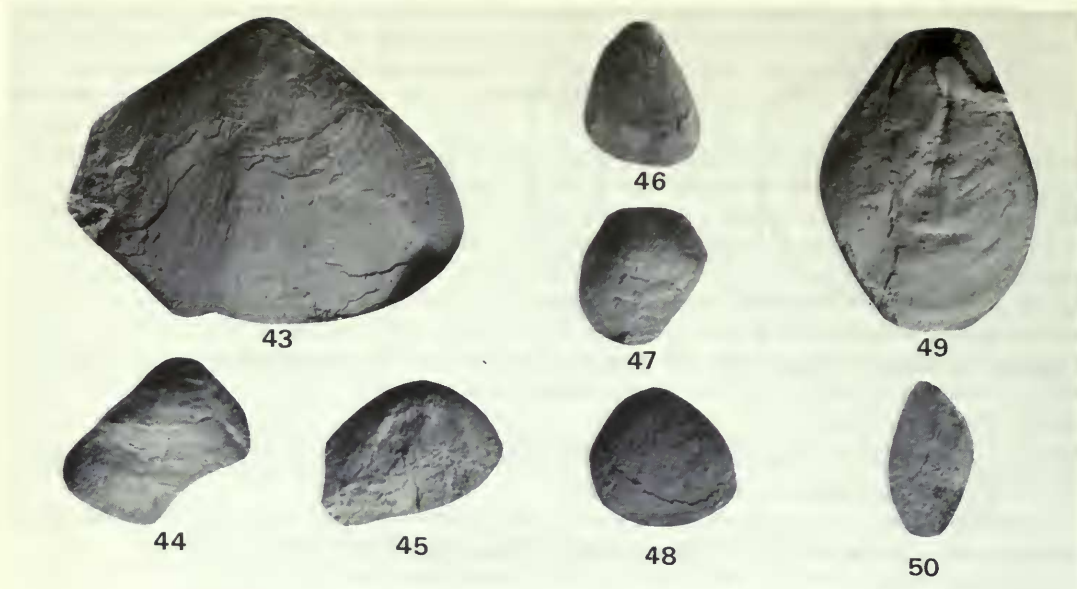
Listed below are the localities from which the specimens, forming the basis of this work, were collected. Following each locality number is the stratigraphic horizon, the National Grid Reference and a short geographical description. Bancroft's localities (1949) are listed where appropriate. Many separate collections derive from a single locality and where appropriate these are mentioned throughout the text.

Alternata Limestone Formation

1. SO 4158 8524. Roadside exposures (north side) 500 m NW of the motte and baily at Cheney Longville.
2. SO 4180 8571. Under both banks of the River Onny, immediately W of footbridge.
3. SO 4182 8569. On the north bank of the River Onny, immediately E of footbridge.
4. SO 4180 8565. Intermittent exposure for 50 m in the south bank of the old Bishops Castle railway cutting.
5. SO 4227 8733. In the roadside immediately SE of Woolston Quarry.
6. SO 4403 9050. Exposure for 45 m in west bank of railway cutting, 650 m N of Marshbrook Station.
7. SO 4772 9182. Soudley Quarry.
8. SO 5137 9741. At the road junction and in the road leading into Chatwall Hall.

Cheney Longville Formation: Glynboro Member

9. SO 4770 9120. Exposure in stream bed SW of Soudley Quarry.
10. SO 4177 8507. Continuous roadside exposure, 250 m NW of the motte and bailey at Cheney Longville.
11. SO 4190 8493. On the eastern side of the road, immediately W of the motte and bailey at Cheney Longville.
12. SO 4207 8546. Large old river cliff; the same beds are exposed in a farm track immediately to the SW.
13. SO 4190 8572. Small roadside quarries, obscured by undergrowth, approximately 250 m SE of New House.
14. SO 4230 8730. On the south side of the road, intermittent exposures 130 m NE of the road junction at Woolston.
15. SO 4357 8922. In the lane 500 m NE of Whittingslow; intermittent exposure for 45 m.
16. SO 4772 9182. Soudley Quarry.



Figs 43–50 *Obolus* sp., exfoliated brachial valves: 43 = BB 72247, $\times 2.2$; 44 = BB 72248, $\times 3.2$; 45 = BB 72246, $\times 2.3$. *Obolus salopiensis* sp. nov., holotype, exfoliated pedicle valve: 46 = BB 72243, $\times 4$; exfoliated brachial valves: 47 = BB 72244, $\times 4.3$; 48 = BB 72245, $\times 6.6$. *Lingulella* sp., exfoliated brachial valves: 49 = B 24201, $\times 3.8$; 50 = BB 72249, $\times 4$.

17. SO 4778 9159. In the stream S of Soudley Quarry.

18. SO 4790 9159. Small roadside exposure SE of Soudley Quarry.

Cheney Longville Formation: Crosspipes Member

19. SO 4190 8493. On the eastern side of the road, immediately W of the motte and bailey at Cheney Longville.
20. SO 4215 8548. In the bed of the River Onny; underwater exposure.
21. SO 4224 8542. River cliff on south side of River Onny; exposure for 50 m, due E of Burrells Coppice.
22. SO 4225 8542. Temporary exposure at end of river cliff on south side of River Onny. Loc. P8 of Bancroft.
23. SO 4240 8725. On the south side of the road, intermittent exposures 50 m NE of the road junction at Woolston.
24. SO 4245 8724. Temporary exposure behind house, immediately N of road junction at Woolston.
25. SO 4250 8729. Outcrop at the junction of the lanes from Woolston to Whittingslow and from Woolston to the Corner, 100 m NE of the T-junction at Woolston.
26. SO 4224 8914. Stream section 750 m due S of Marshbrook.
27. SO 4446 8901. Quarry in Marsh Wood, 740 m due S of Marshbrook.
28. SO 4448 8900. Trackside exposure from Marsh Wood Quarry.
29. SO 4472 8887. Bank of Quinny Brook 350 m SE of Marsh Wood Quarry.
30. SO 4406 8976. Quarry on the south side of the road 180 m WSW of Marshbrook Station.
31. SO 4377 8966. Exposure on the south side of the road 550 m WSW of Marshbrook Station.
32. SO 4398 9002. Roadside exposure 350 m NE of Marshbrook Station on the Marshbrook–Minton road.
33. SO 4507 9094. Stream exposures 300 m S of The Hough.

Acton Scott Formation

34. SO 4230 4040. Under tree roots in abandoned meander of River Onny. Loc. P7 of Bancroft.
35. SO 4252 8600. Small disused quarry next to small stream in Dandy Hollow.
36. SO 4238 8538. Small exposure on south bank of River Onny, partly submerged and at exit of abandoned meander. Locs Pa2 and Pa6 (= Pa' ') of Bancroft.

37. SO 4238 8538. Crumbling riverbank exposure on south side of River Onny and submerged outcrops in river bed.
38. SO 4240 8538. Partly submerged mudstone ledge on south bank of River Onny. Loc. Pa of Bancroft.
39. SO 4241 8538. Partly submerged mudstone ledge, next to dead tree lying across river, on south side of River Onny. Loc. Pm3 of Bancroft.
40. SO 4248 8538. Submerged mudstone ledge on north side of River Onny. Loc. Py2a of Bancroft.
41. SO 4249 8538. Submerged mudstone ledge on north bank of River Onny. Locs Py2g and Py3 of Bancroft.
42. SO 4450 8964. In south bank of boggy stream in wood due E of Rose Villa.
43. SO 4460 8992. Exposure in overflow channel at Chuney Pool, 400 m S of Oakwood.
44. SO 4505 9053. Intermittent exposures in stream between 400 m and 700 m S of The Hough.
45. SO 4645 9013. Exposure in south bank of stream, 1300 m ENE of Acton Scott.
46. SO 4645 9025. Intermittent exposures in tributary streams 120 m N of roadbridge.
47. SO 4496 8955. Disused overgrown quarry 500 m W of Acton Scott Church.
48. SO 4548 8928. Exposure in rock garden of Acton Scott Hall.

Onny Shale Formation

49. SO 4254 8538. Continuous exposure in riverbed of Onny River. Locs Pw1, Pw3 and Pw5 of Bancroft.
50. SO 4257 8537. Continuous exposure in riverbed of Onny River. Loc. Pc of Bancroft denotes base of outcrop.
51. SO 4258 8536. River cliff on north bank of River Onny. Including locs P2 and P3–5 of Bancroft.

Systematic palaeontology

Class **INARTICULATA** Huxley, 1869

Order **LINGULIDA** Waagen, 1885

Superfamily **LINGULACEA** Menke, 1828

Family **OBOLIDAE** King, 1846

Subfamily **OBOLINAE** King, 1846

Genus **OBOLUS** Eichwald, 1829

Obolus salopiensis sp. nov.

Figs 46–48

DESCRIPTION. Dorsibiconvex, subcircular to subtriangular *Obolus* with a mean length relative to width of 93% (range 90% to 94%) and a mean depth relative to length of 11% (range 9% to 12%) for 4 pedicle valves, and a brachial valve 94% as long as wide and 18% as deep as long; both valves strongly convex laterally but flattened medially and anteriorly; shell surface ornamented by very fine concentric growth lines and impersistent low rounded plicae especially on anterior flanks.

Pedicle valve with striated, lenticular pseudointerarea, orthocline in attitude, divided into two propareas by a shallow pedicle groove which is 7.5% (range 6.5% to 8% for 4 valves) as wide as valve length; ventral muscle impressions unknown.

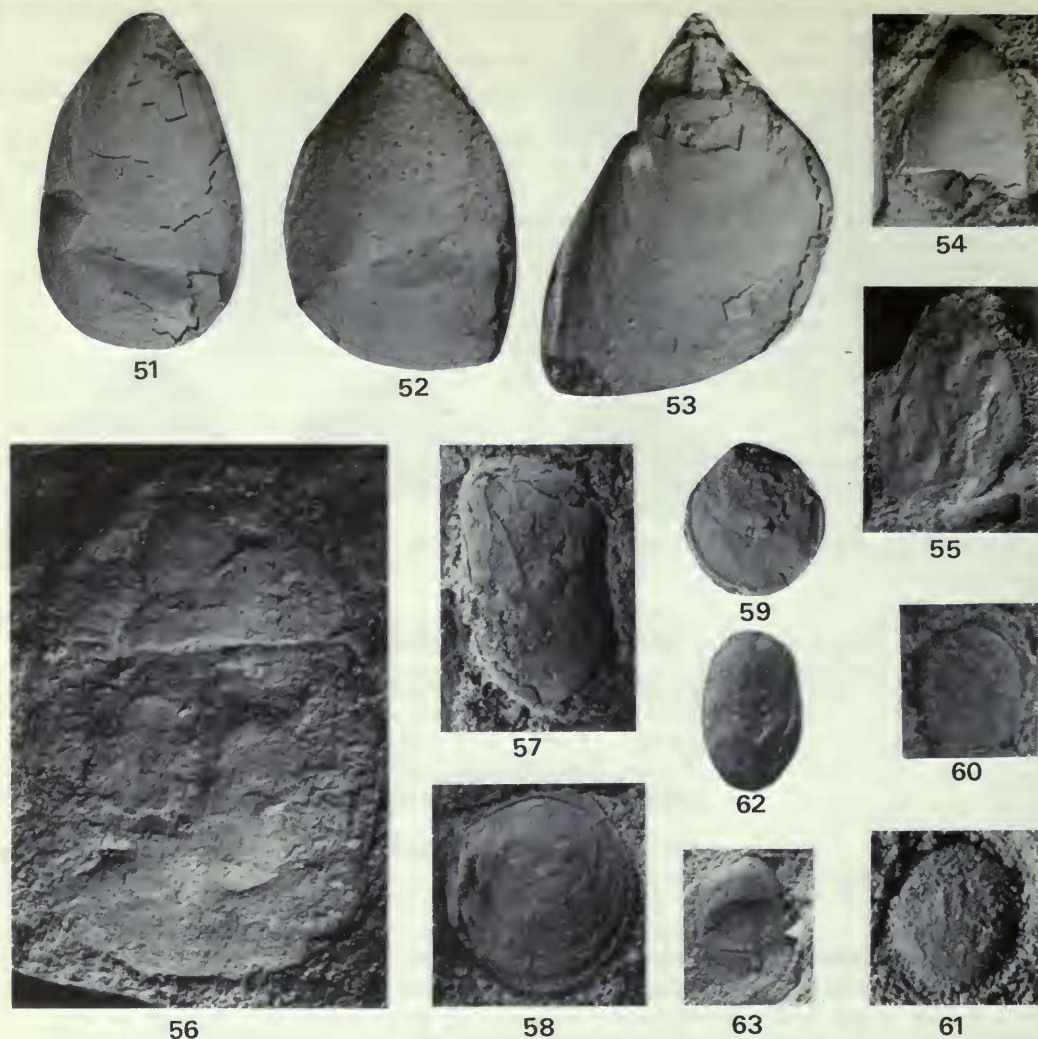
Brachial valve with small striated triangular pseudointerarea, orthocline to anacline in attitude; dorsal muscle impressions unknown.

NAME. From the County of Salop (Shropshire).

MATERIAL. Holotype, partially exfoliated pedicle valve (BB 72243), length 2.8 mm, width 2.9 mm. Paratypes, partially exfoliated brachial valves (BB 72244–5), length 3.0 and 3.8 mm, width 3.3 and 4.2 mm. Type material from loc. 45. Also occurs at locs 35, 36, 43, 44 and 49.

DISCUSSION. This small oboloid occurs sporadically in the Acton Scott Formation and in the lower part of the Onny Shales. Only two small samples, one from each stratigraphic level, were available for bivariate study (Tables 1, 2). * Comparison of dorsal outline of the two samples

*The tables of bivariate statistics are deposit data available in the Palaeontology Library of the British Museum (Natural History); see p. 220.



Figs 51–63 *Palaeoglossa lockleyi* sp. nov., pedicle valves: 51 = BB 72250, $\times 2.7$, 52 = holotype BB 72251, $\times 5.2$, 53 = BB 72252, $\times 5.2$; brachial valves: 54 = BB 72253, $\times 5.4$, 55 = BB 72254, $\times 4$. *Pseudolingula* sp., articulated specimen: 56 = BB 72255, $\times 4.4$. *Paterula* cf. *subcircularis*, pedicle valves: 57 = BB 72258, $\times 12.5$, 59 = BB 72257, $\times 12$; brachial valves: 58 = BB 72259, $\times 10.5$, 60 = BB 72260, $\times 13$. *Paterula* sp., brachial valve: 61 = BB 72261, $\times 7$. *Lingulops* sp., brachial valve: 62 = BB 72264, $\times 7$. *Elliptoglossa* sp.: 63 = BB 72263, $\times 3.3$.

shows a significant difference ($P < 0.01$), with more rounded individuals occurring in the Onny Shales. However, other morphological attributes show no significant differences. The difference in dorsal outline is not sufficient to recognize taxonomically, and thus the samples are thought to indicate the presence of only one morphological species. *O. salopiensis* is closely related to *O. subditivus* Williams but differs in its more triangular shell configuration, shallower pedicle valve and deeper brachial valve. In assigning *O. subditivus* to the obolids, Williams indicated (1974 : 26) that it was a matter of convenience until more was known about the musculature. Similarly, nothing is known about the musculature of *O. salopiensis* so it too is provisionally assigned to the obolids.

Obolus sp.

Figs 43–45

Several exfoliated brachial valves (BB 72246–8) of a large *Obolus* have been obtained from the arenaceous sediments of the Acton Scott Formation at loc. 47. The valves are evenly convex, subtriangular, with a mean length relative to width of 93% (range 85% to 100% for 3 valves) and a mean depth relative to width of 19% (range 15% to 24% for 2 valves). One valve (BB 72246) shows a pair of oval posterior muscle scars but there is no indication as to whether they are transmedian or lateral scars. Shell surface appears to be ornamented by low concentric undulations. The length ranges from 7.1 to 20.0 mm and the width from 8.5 to 24.0 mm.

Subfamily LINGULELLINAE Schuchert, 1893

Genus *LINGULELLA* Salter, 1866*Lingulella* sp.

Figs 49, 50

A few brachial valves of a small *Lingulella* have been recovered from the uppermost Onny Shales at loc. 50. A single brachial valve (B 24201; length 12.2 mm, width 8.2 mm), from the Onny river cliff (loc. 51) occurs in the G. H. Morton collection of the British Museum (Natural History). The valves are elongately oval and 69% as wide as long (range 68% to 70% for 3 valves). One valve was 11% as deep as long. Shell surface ornamented by very fine concentric growth lines. Visceral area strongly pustulose. Owing to the lack of well-preserved material no information is available on the pseudointerareas or muscle configuration, thus precluding specific identification of the specimens.

Genus *PALAEOGLOSSA* Cockerell, 1911*Palaeoglossa lockleyi* sp. nov.

Figs 51–55

DESCRIPTION. Dorsibiconvex oval to elongately oval *Palaeoglossa* with a brachial valve 67% as wide as long and 15% as deep as long (range 13% to 18% for 3 valves); pedicle valve 70% as wide as long and 7% as deep as long (range 6% to 7% for 3 valves); both valves evenly convex, ventral beak not incurved, dorsal beak rounded and incurved; shell surface ornamented by very fine concentric growth lines.

Crescentic ventral pseudointerarea striated, anacline in attitude, 16% as long medially (range 12% to 21%) and 20% as long laterally (range 17% to 21%) as the length of the valve, for three specimens; pedicle trough narrow and shallow; nature of ventral muscle field unknown.

Very small, anacline, dorsal pseudointerarea; muscle field configuration unknown.

NAME. After Dr M. G. Lockley.

DIMENSIONS.

	length	width
Internal mould of pedicle valve, BB 72251, holotype	8.4	5.9
Partially exfoliated pedicle valve, BB 72250	16.5	10.2
Partially exfoliated pedicle valve, BB 72252	9.0 (est.)	8.0
Partially exfoliated brachial valve, BB 72253	4.5	3.5
Partially exfoliated brachial valve, BB 72254	7.0	5.0

HORIZON AND LOCALITIES. Type material from loc. 44, except paratype BB 72250 from loc. 26. Also recorded from locs 35, 36, 43 and 45.

DISCUSSION. A small sample of *P. lockleyi* has been recovered from the Acton Scott Beds to give some indication of shape variability (Tables 3, 4). Comparison of the brachial valve outline with *P. attenuata* (Sowerby), from the Llandeilo Meadowtown and Rorrington Beds of the Shelve district (see Williams 1974 : 34), indicates no significant difference. Comparison of the pedicle valve shape shows that *P. lockleyi* differs significantly ($P < 0.05$) from *P. attenuata* from the

Meadowtown Beds but not from the other samples of *P. attenuata* from the Rorrington Beds and the Upper Llanvirn Betton Beds. *P. lockleyi* and *P. attenuata* further differ in that the former has a deeper brachial and pedicle valve. Also, the pedicle trough of the new species is significantly longer and the ornament consists solely of fine concentric growth lines, there being no indication of fila as in *P. attenuata*.

Subfamily **GLOSSELLINAE** Cooper, 1956

Genus ***PSEUDOLINGULA*** Mickwitz, 1909

Pseudolingula sp.

Fig. 56

Four fragmentary specimens from the Crosspipes Member at Marshwood Quarry (loc. 27) and one from the Acton Scott Formation (loc. 44) are the sole representatives of *Pseudolingula* in the Upper Caradoc. A relatively complete articulated specimen (BB 72255) was 14.5 mm long and 10 mm wide with a biconvex parallel-sided shell. Shell surface appears to have been smooth.

Family **PATERULIDAE** Cooper, 1956

Genus ***PATERULA*** Barrande, 1879

Paterula cf. *subcircularis* Cooper

Figs 57–60

1956 *Paterula subcircularis* Cooper : 239–240; pl. 24, figs 7–10.

DESCRIPTION. Shallow biconvex subcircular *Paterula* with a brachial valve 95% as wide as long and a pedicle valve 93% as wide as long; shell surface ornamented by very fine concentric growth lines; width of shallow pedicle notch 5% of the length of the valve and situated immediately posterior to the ventral beak which is submarginal and located at 12% of the length of the valve; submarginal dorsal beak, located at 11% of the length of the brachial valve.

Well-defined limbus 7% (range 4% to 10% for 7 valves) and 8% (range 5% to 10% for 9 valves) as wide as the pedicle and brachial valves are long, respectively. Pedicle valve with extremely faint short median ridge extending anteriorly from pedicle notch; two lines diverge anteriorly from the beak.

HORIZON AND LOCALITIES. All specimens from the basal Onny Shale Formation; loc. 49. Representative dimensions of pedicle valves: BB 72257, length 1.3 mm, width 1.3 mm; BB 72258, length 2.1 mm, width 2.0 mm. Brachial valves: BB 72259, length 2.0 mm, width 2.0 mm; BB 72260, length 1.1 mm, width 1.1 mm.

Paterula sp.

Fig. 61

Several internal brachial moulds of a paterulid (e.g. BB 72261, length 1.8 mm, width 1.4 mm) have been recovered from the Acton Scott Formation at loc. 44. Two valves were on average 74% as wide as long with a limbus 10% as wide as the valves are long, and a submarginal dorsal beak located at 14% of the length of the valve. Internal features unknown.

DISCUSSION. The Caradoc *Paterula* belong to two distinct species. The sample from the Onny Shale Formation was used to derive the statistics in Tables 5–7. The species is comparable with *P. subcircularis*, described by Cooper (1956 : 239) from the Springtown Shale of Oklahoma, in the near-circular valve shape and shallow biconvexity. However, the Caradoc specimens differ from the large *P. subcircularis* in their small size and in having a shallow pedicle notch as opposed to a deep one. These minor morphological differences do not justify the erection of a new species. No useful purpose is served in comparing the scarce *Paterula* sp. with described species.

Genus *ELLIPTOGLOSSA* Cooper, 1956*Elliptoglossa* sp.

Fig. 63

A single articulated specimen (BB 72263) from the Acton Scott Formation at Chuney Pool (loc. 43) is provisionally assigned to *Elliptoglossa*. The shallow biconvex shell was 4.8 mm long and 4.2 mm wide, with a subelliptical outline and a shell surface ornamented by very fine growth lines.

Genus *LINGULOPS* Hall, 1872*Lingulops* sp.

Fig. 62

Complementary moulds of a brachial valve (BB 72264) from a temporary exposure in the Cross-pipes Member at loc. 24 are the sole representatives of the genus in the Upper Caradoc. The valve, which had a subelliptical outline, was 3.5 mm long, 2.2 mm wide and 0.5 mm deep, with a submarginal beak located 1 mm from the posterior margin. Muscle field anteriorly impressed. Shell surface ornamented by very fine growth lines.

Family *CRANIOPSIDAE* Williams, 1963Genus *PARACRANIOPS* Williams, 1963*Paracraniops doyleae* sp. nov.

Figs 64–69

DESCRIPTION. Oval, subequivalve *Paracraniops* with a dorsal (?) valve 81% as wide as long and 17% as deep as long; transverse profile evenly convex, longitudinal profile eccentrically convex with a submarginal apex slightly overhanging a truncated posterior margin with a small groove; anteriorly flattened. Ventral (?) valve 82% as wide as long and 14% as deep as long; transverse and longitudinal profiles, and apex and posterior margin characteristics as for dorsal (?) valve. Valve edges with small flange about 7% length of valve. Shell surface ornamented by lamellose growth lines which become widely spaced anteromedially.

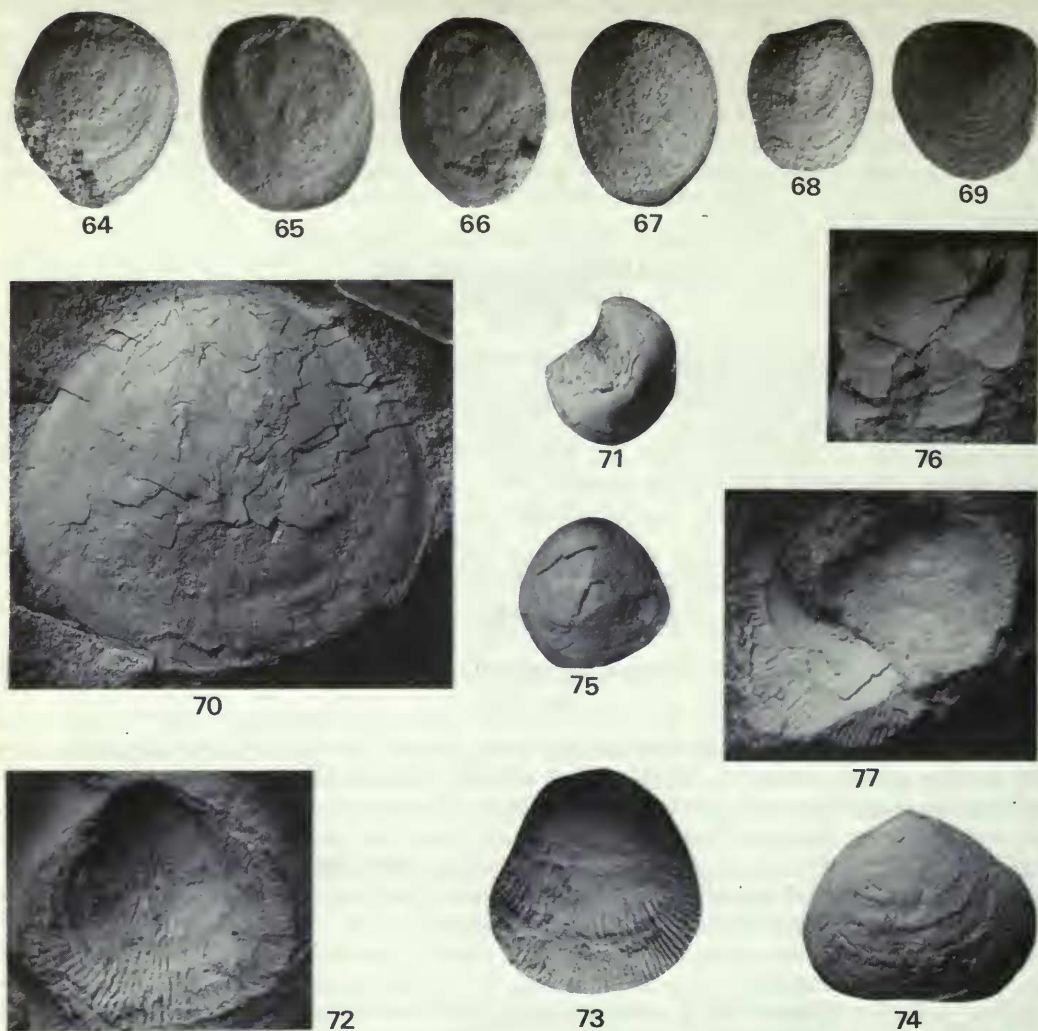
Ventral (?) interior with elongate, semicircular, slightly elevated platform, with well-defined periphery, extending anteriorly from the valve apex for 60% the length of the valve, and containing a pair of posterior adductor scars diverging widely at over 100° from the valve apex, bounded anterolaterally by a pair of elongate oval anterior adductor scars; centre of platform accommodating elongate pear-drop-shaped oblique internal scar.

Dorsal (?) interior with two very poorly defined ridges extending from the valve apex for approximately three-quarters of valve length to the edge of the poorly-defined anterior adductor scar. Posterior adductor and oblique internal scars very poorly developed but appearing to diverge widely from valve apex.

NAME. After Ms M. C. Doyle.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72278, holotype	4.5	4.0
Internal mould of pedicle valve, BB 72279	4.3	3.5
Internal mould of pedicle valve, BB 72280	4.0	3.3
Internal mould of brachial valve, BB 72281	4.5	4.0
Internal mould of brachial valve, BB 72282	3.5	3.0
External mould of brachial valve, BB 72283	4.5	3.9

HORIZON AND LOCALITIES. Type material from loc. 44. Also recorded from locs 11, 12, 15, 19, 24, 26, 30, 32, 34, 35, 43, 45, 46, 47 and 48.



Figs 64-77 *Paracraniops doyleae* sp. nov., internal moulds of pedicle (?) valves: 65 = holotype BB 72278, $\times 6.2$, 67 = BB 72279, $\times 6$, 66 = BB 72280, $\times 6$; internal moulds of brachial valves: 64 = BB 72281, $\times 6$, 68 = BB 72282, $\times 6$, 69 = BB 72283, $\times 5$. *Trematis punctata* (J. de C. Sowerby): 70 = brachial valve BB 54739, $\times 3$, 71 = pedicle valve BB 72256, $\times 1.5$. *Schizocrania salopiensis* Williams, brachial valves: 72 = BB 24955, $\times 3.5$, 73 = BB 24953, $\times 3$, 74 = BB 30077, $\times 3.5$, 75 = BB 72265, $\times 3.5$, 76 = BB 72266, $\times 2.5$, 77 = BB 72267, $\times 3.5$.

DISCUSSION. *Paracraniops* occurs sporadically, but occasionally locally very abundantly, throughout the Cheney Longville Formation and the Acton Scott Formation. Only material from the Acton Scott Formation was well enough preserved for statistical analysis, the results of which are presented in Tables 8-12. The *Paracraniops* from the Cheney Longville Formation is considered conspecific with *P. doyleae*. The Salopian *Paracraniops* is closely related to *P. macella* Williams, which is known from the older Longvillian (Gelli-grin Ashes) rocks of Bala, north Wales (Williams 1963 : 346-349). They principally differ in that the former is more transverse and has a brachial valve deeper than the pedicle valve. Further, in the ventral (?) interior of *P. doyleae* the posterior adductor scars are obtusely splayed and in the dorsal (?) interior the ridges more widely splayed.

Order **ACROTRETIDA** Kuhn, 1949
 Suborder **ACROTRETIDINA** Rowell, 1949
 Superfamily **DISCINACEA** Gray, 1840
 Family **TREMATIDAE** Schuchert, 1893

Genus **TREMATIS** Sharpe, 1848

Trematis punctata (J. de C. Sowerby)
 Figs 70, 71

1839 *Orbicula granulata* J. de C. Sowerby in Murchison : 636.

1839 *Orbicula punctata* J. de C. Sowerby in Murchison : pl. 20, fig. 5.

1866 *Discina (Trematis) punctata* (J. de C. Sowerby) Davidson : 69; pl. 6, fig. 9.

DESCRIPTION. Subcircular, gently convex brachial valve (e.g. BB 54739, length 18.1 mm, width 19.2 mm), about one-sixth as deep as long with maximum depth posteriorly; small dorsal umbo but no pseudointerarea observed on specimens available. Ornament of small hexagonal pits arranged consistently in a hexagonal megapattern. Dorsal interior posteriorly thickened with shallow broad median ridge separating two very shallow oval muscle scars.

Pedicle valve evenly convex, depressed posteriorly, with eccentric beak and open triangular pedicle notch.

HORIZON AND LOCALITIES. Occurs at locs 1, 2, 3, 4, 5, 6, 7 and 8. Lectotype (selected Cocks 1978, not figured here) GSM 6878, from Cheney Longville Formation west of Church Preen.

DISCUSSION. Wright (1963) analysed the pit arrangement of *Trematis*. *T. punctata* has hexagonally arranged pits, and is similar to *T. millepunctata* Hall and *T. craigensis* Reed.

Genus **SCHIZOCRANIA** Hall & Whitfield, 1875

Schizocrania hewardi sp. nov.
 Figs 78–83

DESCRIPTION. *Schizocrania* with subcircular brachial valve, 97% as long as wide and 23% as deep as long, transverse and asymmetric profiles evenly convex; umbo posteriorly placed overhanging straight truncated posterior margin with a strong groove; shell surface ornamented by faint persistent growth lines and straight radial capillae.

Dorsal interior with small elongately oval, widely divergent, posterior adductor scars, weakly impressed and extending anteriorly from the posterior margin for 23% of the length of the valve; anterior adductor not impressed; pedicle valve unknown.

NAME. After Dr A. P. Heward.

DIMENSIONS.	length	width
Exterior of brachial valve, BB 72268, holotype	1.2	1.3
Exterior of brachial valve, BB 72269	1.0	1.2
Exterior of brachial valve, BB 72270	1.1	1.2
Exterior of brachial valve, BB 72271	1.1	1.2

HORIZON AND LOCALITY. All the material from the upper part of the Onny Shale Formation, from the Onny river cliff; loc. 51.

Schizocrania salopiensis Williams
 Figs 72–77

1974 *Schizocrania salopiensis* Williams : 44–46; pl. 6, figs 22–26.

DESCRIPTION. *Schizocrania* with subcircular to subelliptical or subtriangular brachial valve, 95% as long as wide and 29% as deep as long, evenly convex in both transverse and longitudinal profile; submarginal umbo not overhanging smoothly rounded posterior part of valve; shell

surface ornamented by very faint impersistent growth lines and radial capillae, which branch dichotomously and curve towards the anterior and lateral margins.

Dorsal interior with large slightly divergent subcircular to oval posterior adductor scars, weakly impressed and extending anteriorly from the posterior margin for 29% of the length of the valve; small circular anterior adductor scars situated near the centre of the valve and separated by a very shallow median ridge; pedicle valve unknown.

HORIZON AND LOCALITIES. BB 72265–7 are from loc. 44; BB 24953, BB 24955 and BB 30077 from loc. 27. Also recorded at locs 36 and 45. Dimensions of brachial valves ranged from BB 72265, with length 4.6 mm and width 5.5 mm, to BB 24953, length 12.6 mm and width 10.4 mm.

DISCUSSION. *Schizocrania* brachial valves are fairly common in the Upper Caradoc rocks, which have provided two samples used to derive the statistics given in Tables 13–15. Data on shell shape, depth and length of posterior adductor scars show that *S. hewardi* differs from *S. salopiensis* Williams (1974 : 46) in valve shape ($P < 0.01$) and length of the posterior adductor scars ($P < 0.05$). They do not differ in shell depth. Further, *S. hewardi* has an incurved posteriorly-placed umbo along a straight truncated valve margin with a strong groove, whilst *S. salopiensis* has a rounded posterior profile without an overhanging umbo. The posterior adductor scars of *S. hewardi* are also more widely splayed.

S. hewardi differs from *S. salopiensis* Williams, from the Upper Llandeilo Rorrington Beds of the Shelve district, in terms of valve shape ($P < 0.001$), depth ($P < 0.001$) and length of posterior adductor scars ($P < 0.05$). From the younger sample of *S. salopiensis* from the Lower Caradoc Spy Wood Grit *S. hewardi* differs in valve shape ($P < 0.001$) and length of posterior adductor scars ($P < 0.05$). There is no difference in valve depth of the two species. Such differences are considered sufficiently important to warrant the erection of a new species, even though no pedicle valves of either species have yet been recovered.

The *Schizocrania* from the Crosspipes Member and Acton Scott Formation is similar to *S. salopiensis* in respect of its rounded rather than truncated posterior margin and submarginal umbo. However, it differs significantly ($P < 0.05$) from both the Spy Wood Grit and Rorrington Beds samples of *S. salopiensis* (see Williams 1974 : 46) in shell shape as it grew longer relative to width. This difference is not considered sufficiently important to warrant the erection of a new species.

Family DISCINIDAE Gray, 1840

Subfamily ORBICULOIDEINAE Schuchert & Le Vene, 1929

Genus ORBICULOIDEA d'Orbigny, 1847

Orbiculoidea ovata sp. nov.

Figs 84–88

DESCRIPTION. Biconical, subcircular to suboval *Orbiculoidea* with a brachial valve on average 92% as wide as long (range 76% to 99% for 5 valves), 27% as deep as long (range 27% to 31% for 5 valves); transverse profile evenly convex, longitudinal profile eccentrically convex with a beak located on average 37% (range 29% to 41% for 5 valves) of the length of the brachial valve; pedicle valve on average 86% as wide as long (values for 2 valves 80% and 92%), 23.5% as deep as long (values for 2 valves 23% and 24%); transverse profile evenly convex, longitudinal profile eccentrically convex with a conical beak located 39% (value for 2 valves 39% each) of the length of the pedicle valve, which is flattened anteriorly; surface of both valves ornamented solely by coarse well-rounded concentric growth lines.

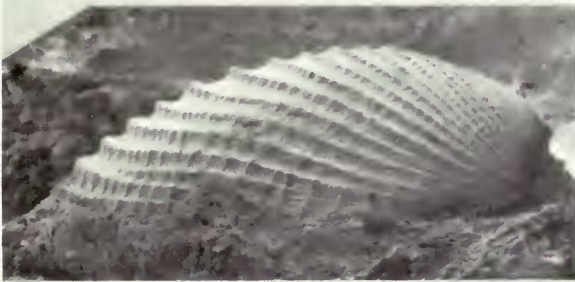
Figs 78–83 *Schizocrania hewardi* sp. nov., all brachial valves: 79 and 81 = holotype, BB 72268, viewed from above and obliquely, $\times 75$; 78 and 80 = BB 72271, viewed half obliquely and from side, $\times 75$ and $\times 100$ respectively; 82 = BB 72269, partly exfoliated valve viewed from above, $\times 100$; 83 = oblique enlargement of ornament on BB 72271, $\times 400$. Figs 78–83 are all stereoscan photomicrographs with approximate magnifications.



78



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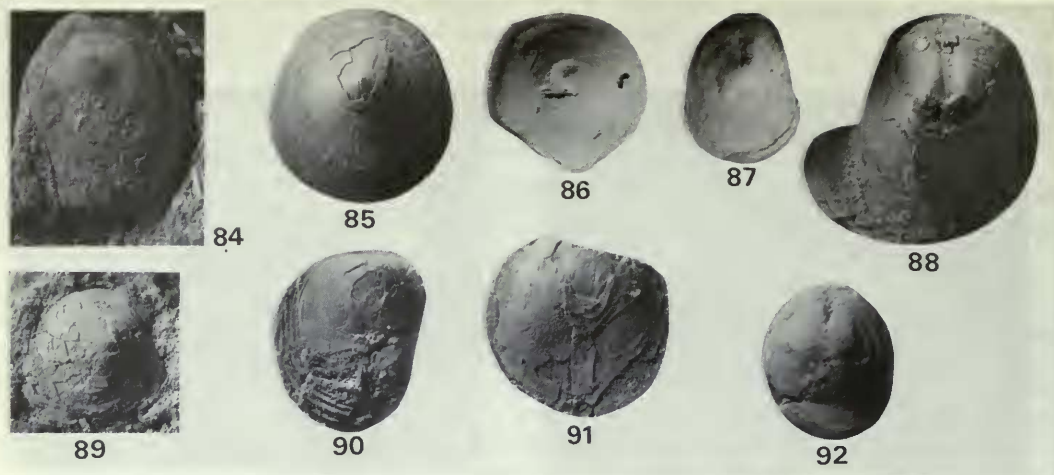
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Figs 84-92 *Orbiculoidea ovata* sp. nov., brachial valves: 84 = BB 72274, $\times 2.5$, 85 = **holotype** BB 72273, $\times 2.7$, 86 = BB 24949, $\times 2$; pedicle valves: 87 = BB 72275, $\times 3$, 88 = BB 31260, $\times 2.7$. *Orbiculoidea* sp.: 89 = brachial valve BB 24948, $\times 3.3$. *Schizotreta* sp. 1: 92 = pedicle valve BB 24950, $\times 8.5$. *Schizotreta* sp. 2, brachial valves: 90 = BB 72276, $\times 3.5$, 91 = BB 72277, $\times 3$.

Dorsal interior with very indistinct muscle impressions anterior of apex and from which two indistinct pallial tracks extend anterolaterally.

Ventral interior smooth and with pedicle groove extending posteriorly from the umbo for 31% (values for 2 valves 31% each) of the length of the valve.

DIMENSIONS.	length	width
Exterior of brachial valve, BB 72273, holotype	9.8	9.2
Exterior of brachial valve, BB 72274	8.7	8.6
Exterior of pedicle valve, BB 72275	6.5	5.2
Partially exfoliated pedicle valve, BB 31260	11.5	10.0
Internal mould of brachial valve, BB 24949	11.5	11.0

HORIZON AND LOCALITIES. BB 72273-4 from type locality, loc. 44. Paratypes BB 24949 from loc. 47, BB 72275 from loc. 48 and BB 31260 from well excavation at Plaish. Also recorded from locs 35 and 43.

Orbiculoidea sp.

Fig. 89

There is a partially exfoliated brachial valve in the BM(NH) collection (BB 24948) from calcareous sediments of the Acton Scott Formation at Batch Gutter in the Onny Valley (SO 4245 8538). The valve, which was 6.0 mm long, 5.7 mm wide and 1.6 mm deep, was subcircular in outline with the beak situated 2.2 mm forward of the posterior margin. The transverse profile was evenly convex and the external surface ornamented by two sets of fila, one very fine and on average 2 mm apart and the other intercalated and very impersistent. *Orbiculoidea* occurs sparsely in Upper Caradoc rocks of east Salop. Most specimens belong to the new species *O. ovata*, which differs from the present *Orbiculoidea* sp. only in details of the ornament.

Genus *SCHIZOTRETA* Kutorga, 1848

Schizotreta sp. 1

Fig. 92

An internal mould of a pedicle valve in the BM(NH) collection (BB 24950) is the sole representative of *Schizotreta* sp. 1. It is from the Onny Shale Formation of the Onny river cliff, loc. 51. The

valve, which was approximately 3.1 mm long, 2.2 mm wide and 0.6 mm deep, was oval in outline with the low depressed beak situated 1.0 mm forward of the truncated posterior margin. The transverse profile was evenly convex and the external surface ornamented by coarse fila.

Schizotreta sp. 2

Figs 90, 91

Two partially exfoliated brachial valves (BB 72276–7) from loc. 44 of the Acton Scott Formation are the only representatives of *Schizotreta* sp. 2 from the east Salop Upper Caradoc. BB 72276, 5.5 mm long, 5.3 mm wide and 1.1 mm deep, is suboval in outline with a rounded anterior margin, parallel lateral margins and a truncated posterior with a slightly overhanging marginal beak; its internal features are unknown. The shell surface is ornamented by very coarse concentric ridges. BB 72277a, b, a fragmentary specimen, is 7 mm wide and over 7.5 mm long and 1.5 mm deep.

DISCUSSION. It is considered unlikely that *Schizotreta* sp. 1 and sp. 2 are conspecific, because of their difference in ornament. In the development of strong coarse concentric ridges, submarginal beak and truncated posterior margin *Schizotreta* sp. 2 closely resembles the older *S. corrugata* Cooper from the Porterfield Pratt Ferry Formation of Alabama (Cooper 1956 : 277).

Class **ARTICULATA** Huxley, 1869

Order **ORTHIDA** Schuchert & Cooper, 1932

Suborder **ORTHIDINA** Schuchert & Cooper, 1932

Superfamily **ORTHACEA** Woodward, 1852

Family **ORTHIDAE** Woodward, 1852

Subfamily **PRODUCTORTHINAE** Schuchert & Cooper, 1931

Genus *NICOLELLA* Reed, 1917

Nicolella actoniae (J. de C. Sowerby)

1839 *Orthis actoniae* J. de C. Sowerby in Murchison : 639; pl. 20, fig. 16 (left); *non* pl. 20, fig. 16 (right).

1963 *Nicolella actoniae* (J. de C. Sowerby); Williams : 352–356; pl. 1, figs 15–19.

cf. 1974 *Nicolella* cf. *actoniae* (J. de C. Sowerby); Williams : 57–58; pl. 9, figs 1–6.

cf. 1977 *Nicolella* cf. *actoniae* (J. de C. Sowerby); Mitchell : 31–32; pl. 3, figs 14–20.

Williams (1963) has redescribed and figured *N. actoniae*, and his work will not be duplicated here. He records the species definitely from loc. 45, where in my collections it is rare, and possibly from loc. 47, where I have not found it. It also occurs at loc. 43 and abundantly at loc. 44. All these localities are in the Acton Scott Formation.

Family **DOLERORTHIDAE** Öpik, 1934

Genus *DOLERORTHIS* Schuchert & Cooper, 1931

Dolerorthis virgata (J. de C. Sowerby)

Figs 93–105

1839 *Orthis virgata* J. de C. Sowerby in Murchison : 639; pl. 20, fig. 15.

1869 *Orthis calligramma* var. *virgata* J. de C. Sowerby; Davidson : 240 *pars*; pl. 35, figs 23, 24, *non* figs 1–22.

1869 *Orthis virgata* J. de C. Sowerby; Davidson : 240; pl. 37, fig. 2.

1958 *Dolerorthis duftonensis* (Reed); Dean : pl. 25, fig. 1.

1978 *Dolerorthis virgata* (J. de C. Sowerby); Cocks : 45.

DESCRIPTION. Subcircular to subquadrate, unequally bioconvex *Dolerorthis* with rectangular cardinal margins; brachial valve 76% as long as wide, evenly convex, non-sulcate and 14% as deep as long; dorsal interarea anacline, notothyrium open; pedicle valve 84% as long as wide,

evenly convex and 24% as deep as long; long apscaline interarea, delthyrium open; ornamentation costellate commonly with two ribs per mm, 10 mm anteromedially of the dorsal umbo, cancelled by fine concentric lamellae.

Ventral muscle scar subpentagonal, extending anteriorly for 35% of the length of the valve and 30% as wide as the valve is long; lanceolate adductor scar not surrounded by diductor tracks; teeth strong, supported by short subparallel dental lamellae extending anteriorly of umbo for 17% of the valve length.

Dorsal interior with simple ridge-like cardinal process; brachioophores simple, stout, widely divergent with their bases extending anteriorly of the dorsal umbo for 16% of the valve length and splaying laterally for 33% of the valve length; dorsal adductor field quadripartite with posterior scars larger than anterior and extending anteriorly for 50% of the length of the valve.

MATERIAL. Lectotype (selected Cocks 1978: 45) GSM Geol. Soc. Coll. 6904 (Fig. 95), length 17.9 mm, width 22.2 mm, from calcareous sandstones at Acton Scott, possibly locs 47 or 48. Other material from loc. 12, coll. O18 (e.g. Figs 93, 102, BB 72395, length 19.8 mm and width 25.0 mm, and Fig. 94, BB 72396, length 14.5 mm and width 19.0 mm), O112 (e.g. Fig. 100, BB 72397, length 24 mm and width 26.0 mm, and Fig. 105, BB 72398, length 9.8 mm and width 13.8 mm) and O19 (e.g. Fig. 97, BB 72399 and Fig. 104, BB 72400); also loc. 27, coll. M20 (e.g. Fig. 98, BB 72401, Fig. 103, BB 72402, Fig. 99, BB 72403 and Fig. 96, BB 72404); also loc. 40, coll. O103 (e.g. Fig. 101, BB 72405) and locs 10, 11, 17, 32, 41 and 48.

DISCUSSION. *Dolerorthis* occurs sparingly in the Upper Caradoc, but the small samples have been combined to obtain the statistics in Tables 16–25. The sample from the Alternata Limestone and Glynboro Member does not differ in terms of the known bivariate characteristics from the Crosspipes Member and Acton Scott Formation sample, although a larger collection may show the later sample to consist of slightly more coarsely-ribbed individuals. However, such a minor difference is not taxonomically important, so all Upper Caradoc *Dolerorthis* are included in *D. virgata*.

D. virgata differs from *D. duftonensis prolixa* Williams in a number of characters, namely in having a relatively longer brachial valve ($P < 0.01$), a slower increase in depth of the brachial valve ($P < 0.02$), relatively longer dorsal cardinalia ($P < 0.01$) and a slower increase in length of the dorsal muscle field ($P < 0.01$). *D. virgata* does not differ in any of its statistical data from those given by Williams (1963: 60–61) for *D. duftonensis*. However, there may be significant differences between the two as the former species appears to have a shallower pedicle valve and a longer ventral muscle field. *D. duftonensis* could be a synonym of *D. virgata*, but until more is known about the variation of *D. duftonensis* the two species are kept separate.

Family DINORTHIDAE Schuchert & Cooper, 1931

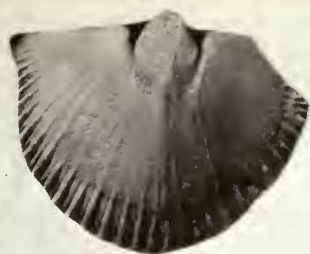
Genus DINORTHIS Hall & Clarke, 1892

Dinorthis sp.

Figs 106, 111

DESCRIPTION. Subquadrate, dorsibiconvex *Dinorthis* with a brachial valve 76% as long as wide and 26% as deep as long; pedicle valve weakly convex with slightly raised umbonal region, and

Figs 93–111 *Dolerorthis virgata* (J. de C. Sowerby), internal moulds of pedicle valves: 93 = BB 72395a, $\times 1.6$, 94 = BB 72396, $\times 2.6$, 95 = lectotype, GSM 6904, $\times 2$, 96 = BB 72404, $\times 1.1$, 97 = BB 72399, $\times 1.2$, 99 = BB 72403, $\times 1.1$; external mould of pedicle valve: 102 = BB 72395b, $\times 2.5$; internal moulds of brachial valves: 98 = BB 72401, $\times 1.3$, 100 = BB 72397, $\times 1.5$, 101 = BB 72405, $\times 2$, 103 = BB 72402, $\times 1.2$, 104 = BB 72400, $\times 2$, 105 = BB 72398, $\times 2$. *Dinorthis* sp., internal mould of pedicle valve: 106 = BB 72407, $\times 1.5$; internal mould of brachial valve: 111 = BB 72406, $\times 0.8$. *Platystrophia* sp. 1, internal mould of pedicle valve: 107 = BB 72394, $\times 1$; internal moulds of brachial valves: 108 = BB 72368, $\times 2$, 109 = BB 72367, $\times 1.2$. *Platystrophia* sp. 2, internal mould of brachial valve: 110 = BB 72369, $\times 3.5$.



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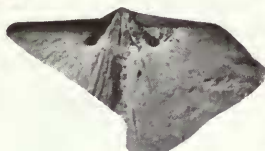
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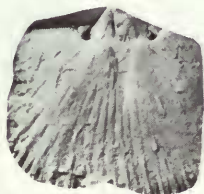
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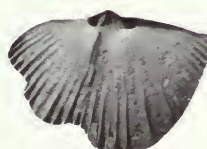
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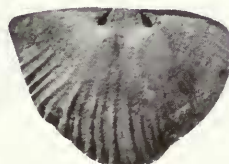
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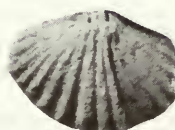
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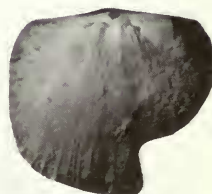
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111

73% as long as wide; ventral interarea apscaline, dorsal interarea orthocline; radial ornamentation of strong costae; ventral muscle scar elongately subrectangular, 40% as long as the valve and 28% as wide as the valve is long; teeth blunt and supported by short dental lamellae extending anteriorly for 15% of the valve length; cardinal process differentiated into short stout shaft and expanded myophore; brachiophores stout, unsupported and extending forward of dorsal umbo for 15% the length of the valve and splaying laterally for 29% the length of the valve; dorsal adductor field suboval, weakly impressed and extending anterior of dorsal umbo for about half the length of the valve.

HORIZON AND LOCALITIES. BB 72406, brachial valve (length 28.7 mm, width 38.0 mm) from loc. 29, BB 72407, pedicle valve (length 15.4 mm, width 21.2 mm) from loc. 13. Also recorded from locs 15, 18, 30 and 32.

Family **PLECTORTHIDAE** Schuchert & Le Vene, 1929

Subfamily **PLATYSTROPHIINAE** Schuchert & Le Vene, 1929

Genus **PLATYSTROPHIA** King, 1850

Platystrophia sp. 1

Figs 107–109

The only specimens, from the Crosspipes Member, are an incomplete complementary external and internal mould of a brachial valve (BB 72367; loc. 24, colln WFT2), a complete internal mould (BB 72368; loc. 24, colln WFT1) and an internal mould of a pedicle valve (BB 72394; loc. 27, colln M6). The brachial valves were 68% as long as wide and 33% as deep as long with a well-defined slightly rounded fold about 34% as wide as the valve. The radial ornamentation consisted of four costae on the fold and five on each lateral slope, with a wavelength of 1 mm, 5 mm anteromedially of the dorsal umbo. Cardinal process ridge-like; short, thick, slightly divergent brachiophores bound wide notothyrium, extending anteriorly for 17% of the length of the valve and splaying laterally for 34% of the valve length; dorsal adductor scars strongly impressed, quadripartite, extending anteriorly for 49% the length of the valve on either side of a low thin median ridge. The pedicle valve was 25 mm wide, 20.2 mm long and 6 mm deep, with an elongately oval, subtriangular muscle field 32% as long as the valve and 18% as wide as the valve is long; small thick pedicle callist; teeth stout, supported by short dental plates extending anteriorly for 16% the length of the valve.

Platystrophia sp. 2

Fig. 110

The only specimen, from the Acton Scott Formation, is an internal mould of a brachial valve (BB 72369; loc. 43, colln CP3). The valve, which was 4.7 mm long, 6.7 mm wide and 1.7 mm deep,

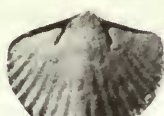
Figs 112–144 *Rhactorthis grandis* sp. nov., internal moulds of pedicle valves: 113 = BB 72349, $\times 2$, 114 = BB 72351, $\times 3.7$, 115 = BB 72353, $\times 3$, 116 = BB 72352, $\times 3$, 117 = BB 72357, $\times 4$, 118 = BB 72354a, $\times 3.3$, 120 = BB 72350, $\times 4$; partially conjoined valves, **holotype**: 112 = BB 72348, $\times 4$; external mould of pedicle valve: 119 = BB 72354b, $\times 3.3$; internal and external moulds of brachial valves: 121 = BB 72359a, $\times 2.5$, 122 = BB 72359b, $\times 2.5$, 123 = BB 72362, $\times 2.3$, 124 = BB 72361b, $\times 3$, 125 = BB 72361a, $\times 3$, 126 = BB 72358, $\times 3.2$, 127 = BB 72360, $\times 2.7$, 128 = BB 72356, $\times 5$, 129 = BB 72355, $\times 5.3$, 130 = BB 72363, $\times 3$. *Rhactorthis actoniae* sp. nov., **holotype**, internal mould of pedicle valve: 131 = BB 72364, $\times 1.5$; internal and external moulds of brachial valves: 132 = BB 72365, $\times 3.3$, 133 = BB 72366a, $\times 2$, 134 = BB 72366b, $\times 2.2$. *Rhactorthis* cf. *crassa* Williams, internal and external moulds of pedicle valves: 135 = BB 72381, $\times 3.2$, 136 = BB 72380, $\times 2$, 137 = BB 72382, $\times 6.5$, 138 = BB 72379a, $\times 4.5$, 139 = BB 72379b, $\times 4.5$; internal moulds of brachial valves: 140 = BB 72377, $\times 5$, 141 = BB 72376, $\times 2$, 142 = BB 72378, $\times 5.5$. *Gelidorthis* sp., internal mould of pedicle valve: 143 = BB 72373, $\times 5$. *Plectorthid* gen. et sp. indet., internal mould of pedicle valve: 144 = BB 72374, $\times 3$.



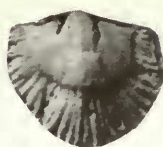
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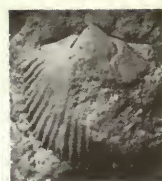
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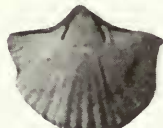
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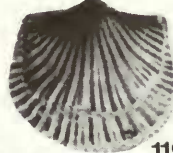
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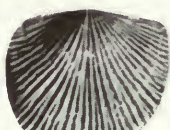
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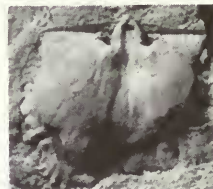
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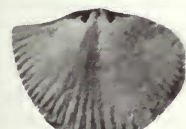
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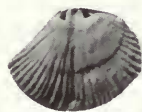
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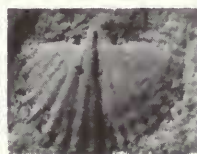
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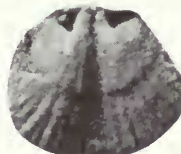
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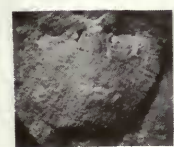
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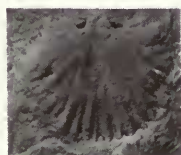
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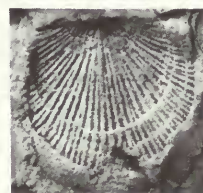
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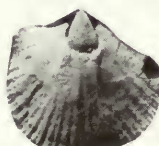
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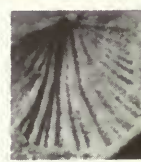
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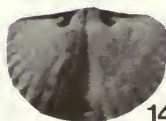
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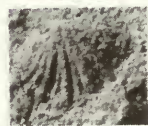
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had a poorly-developed rounded sulcus 2.5 mm wide. Radial ornamentation of three costae on the fold and seven on each lateral slope. Cardinal process ridge-like, brachiophore bases subparallel and extending anteriorly for 13% the length of the valve; fulcral plates present.

Subfamily **RHACTORTHINAE** Williams, 1963

Genus **RHACTORTHIS** Williams, 1963

TYPE SPECIES. *Rhactorthis crassa* Williams, 1963 by original designation.

Rhactorthis actoniae sp. nov.

Figs 131–134

DESCRIPTION. Subcircular unequally biconvex *Rhactorthis* with sulcate brachial valve, 80% as wide as long and 20% as deep as long; evenly convex pedicle valve 83% as wide as long and 25% as deep as long, pedicle interarea slightly curved apscaline, brachial interarea straight anacline; delthyrium and notothyrium open; radial ornamentation commonly of five costellae (measured on 4 valves) per mm, 2 mm anteromedially of the dorsal umbo, commonly arising by dichotomous branching; disruptive growth lines occasionally present.

Ventral muscle scar subpentagonal and extending anteriorly for 30% the length of the valve and 33% as wide as the valve is long; diductor scar does not surround median adductor scar; teeth small, supported by receding dental lamellae and extending anteriorly for 18% the length of the valve.

Dorsal interior with very shallow median ridge, at posterior end of which arises continuous shaft of cardinal process which is crenulated posteriorly, fills notothyrium and projects slightly beyond hinge line; brachiophores very short, divergent and extending anteriorly for 17% the length of the valve, with delicate convergent bases which curve laterally parallel to hinge line for 34% the length of the valve; adductor scars very weakly impressed, elongately oval and extending anteriorly for 44% the length of the valve.

NAME. Referring to the locality near Acton Scott.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72364, holotype	6.5	12.0
Internal mould of brachial valve, BB 72365	5.1	6.0
External and internal moulds of brachial valve, BB 72366a, b	9.6	10.7

HORIZON AND LOCALITIES. Type material from loc. 47, colln CF3, the only locality from which the species has been recovered.

DISCUSSION. See under *R. grandis*, p. 239.

Rhactorthis cf. *crassa* Williams

Figs 135–142

cf. 1963 *Rhactorthis crassa* Williams : 372–375; pl. 4, figs 1–6.

DESCRIPTION. Subcircular to subquadrate, moderately biconvex *Rhactorthis* with weakly sulcate brachial valve 82% as wide as long and 25% as deep as long, lateral slopes moderately strong, evenly convex with shallow rounded sulcus originating at umbo; pedicle valve moderately convex, 82% as wide as long and 32% as deep as long; ventral interarea apscaline, dorsal interarea anacline; delthyrium and notothyrium open; radial ornamentation of five to eight low angular costellae per mm, 2 mm anteromedially of the dorsal umbo, arising by dichotomous branching; internal branching common, externals not observed; concentric lamellae common, but no major disruption by growth lines.

Ventral muscle scar elongately subpentagonal and extending anteriorly for 32% of the valve length and 28% as wide as the valve is long; adductor scar not surrounded anteriorly by diductor

impressions; teeth small and supported by short divergent dental lamellae extending anteriorly for 20% of the valve length; dental lamellae continued along sides of muscle field as shell ridges and meet anteromedially to surround muscle field completely.

Dorsal interior with wide rounded median ridge; cardinal process shaft broad and continuous with posterior end of median ridge; myophore crenulated, completely filling notothyrium and extending slightly beyond hinge line; subparallel to divergent short, stout brachioophores extending anteriorly for 17% the length of the valve, with convergent bases which sometimes curve laterally for 43% of the length of the valve; sockets small and deep; adductor scars very weakly impressed, situated on either side of median ridge and extending anteriorly for 45% of the valve length.

MATERIAL AND LOCALITIES. Loc. 43, colln CP4 (e.g. Fig. 141, BB 72376, length 8.5 mm, width 9.6 mm), colln CP1 (e.g. Fig. 136, BB 72380, length 9.0 mm, width 10.0 mm and Fig. 142, BB 72378) and CP2 (e.g. Fig. 135, BB 72381). Loc. 45, colln AS4 (e.g. Fig. 140, BB 72377, length 3.2 mm, width 4.0 mm and Figs 138–9, BB 72379, length 4.5 mm, width 5.2 mm) and colln AS6 (e.g. Fig. 137, BB 72382, length 2.6 mm and width 3.1 mm.)

Rhactorthis grandis sp. nov.

Figs 112–130

DESCRIPTION. Subcircular, strongly biconvex *Rhactorthis* with strongly sulcate brachial valve 78% as wide as long and 23% as deep as long, lateral slopes strong, evenly convex and with deep, persistent, rounded sulcus originating at umbo; pedicle valve strongly convex, sometimes strongly carinate, 84% as wide as long and 33% as deep as long; apscaline ventral interarea over one-fifth as long as the pedicle valve; anacline dorsal interarea over one-eighth as long as dorsal valve; delthyrium and notothyrium open; radial ornamentation commonly of five or six costellae per mm, 2 mm anteromedially of the dorsal umbo, arising by dichotomous branching, externals rarely developed, internals common; growth lines lamellose with occasional large disruptive growth lines.

Ventral muscle scar rounded subpentagonal and extending anteriorly for 31% the length of the valve and 34% as wide as the valve is long; wide adductor scar not surrounded anteriorly by diductor impressions; teeth small and supported by very short, delicate dental lamellae extending anteriorly for 19% the length of the valve.

Dorsal interior with well-developed ridge posteriorly; wide ridge-like cardinal process continuous with median ridge and posteriorly crenulated, filling notothyrium, projecting slightly beyond hinge line; divergent, short brachioophores extending anteriorly for 16% the length of the brachial valve and with convergent bases which curve laterally away from median plane, for 37% the length of the valve, parallel with hinge line to define small deep sockets; adductor scars very weakly impressed, situated on either side of median ridge, immediately anterior of the brachioophores and extending anteriorly for 48% the length of the valve.

DIMENSIONS.	length	width
BB 72348, holotype, pedicle valve (Fig. 112)	5.0	5.8
holotype, brachial valve	4.3	5.8
BB 72349, pedicle internal mould (Fig. 113)	5.8	8.2
BB 72350, pedicle internal mould (Fig. 120)	3.2	4.5
BB 72352, pedicle internal mould (Fig. 116)	6.5	6.6
BB 72355, brachial external and internal mould (Fig. 129)	3.8	4.5
BB 72363, brachial external and internal mould (Fig. 130)	5.9	7.0
BB 72359, brachial external and internal mould (Fig. 121)	7.6	8.6

LOCALITIES. BB 72348–53 and BB 72359–62 from loc. 25, colln WFT7; BB 72354 from loc. 25, colln WFT9; BB 72355–8 and BB 72363 from loc. 28, colln M11. Also recorded from locs 22 and 33.

DISCUSSION. Four samples of *Rhactorthis* have been assessed statistically, and the data set out in Tables 26–35. *Rhactorthis* from locs 25 (A in tables) and 28 (B in tables) in the *O. reuschi* Zone of the Crosspipes Member do not differ in their bivariate characteristics and consequently are treated as representing a single new species, *R. grandis*.

R. actoniae differs from *R. grandis* from loc. 25 in having a slower increase in depth of the pedicle valve ($P < 0.01$) and in a relatively narrower ventral muscle field ($P < 0.05$). *R. actoniae* differs from *R. grandis* from loc. 28 in having a relatively narrower ventral muscle field ($P < 0.01$) and a slower increase in length of the dorsal muscle field ($P < 0.05$). Further, the pedicle valves of *R. actoniae* are moderately evenly convex whereas those of *R. grandis* are often carinate, resembling *R. melmerbiensis* (Reed) from the Dufton shales (Reed 1910 : pl. 23), but not as deep (Williams 1963 : 375). The two species further differ in the configuration of the dorsal cardinalia, with *R. melmerbiensis* apparently possessing shorter brachiophores whose bases do not splay to run parallel to the hinge line.

R. crassa Williams, the type species of the genus, from the Gelli-grin Calcareous Ashes (Longvillian), differs from *R. grandis* in having relatively wider dorsal cardinalia ($P < 0.001$ with loc. 25 and $P < 0.01$ with loc. 28 *R. grandis*). Further, *R. grandis* has a carinate pedicle valve. *R. grandis* has fine radial ornamentation with counts of 5, 6 and 7 ribs per mm, 2 mm anteromedially of the dorsal umbones of 8, 8 and 1 specimens respectively, figures which are comparable to the costae counts derived from the published photographs of *R. crassa* (Williams 1963 : pl. 4) but not consistent with the species description (see Williams 1963 : 374). The brachial valve of *R. grandis* has 3*a* arising earlier than 1*a* and earlier than 2*a* in 4 out of 5 and 5 out of 5 specimens respectively; these proportions are significantly different from those in *R. crassa* ($P < 0.2$ and $P < 0.02$ respectively).

R. cf. crassa differs from *R. grandis* in the faster relative increase in length of the dorsal cardinalia ($P < 0.05$ – 0.02) and length of the adductor scar ($P < 0.05$), relatively shallow pedicle valve ($P < 0.05$) and relatively longer pedicle muscle field ($P < 0.02$). From *R. actoniae*, *R. cf. crassa* differs in having a relatively longer brachial valve ($P < 0.05$) and relatively shorter dorsal muscle field ($P < 0.05$). Further, the ribbing of *R. cf. crassa* is fine, having 5, 6, 7 and 8 costellae per mm, 2 mm anteromedially of the dorsal umbo on 2, 1, 1 and 1 shells respectively. This distribution is significantly finer than in *R. grandis* ($P < 0.03$), and in *R. actoniae* ($P < 0.05$) which has 4 costellae at the appropriate distance from the dorsal umbo on 4 shells.

R. cf. crassa differs from *R. crassa* only in having a significantly ($P < 0.02$) faster increase in length of the ventral muscle field. This difference is not sufficient to warrant the erection of a new species, so the specimens of *Rhactorthis* from the Actonian siltstones of locs 43 and 45 are referred to *R. cf. crassa*.

Subfamily PLECTORTHINAE Schuchert & Le Vene, 1929

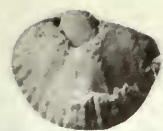
Genus *GELIDORTHIS* Havlíček, 1971

Gelidorthis sp.

Fig. 143

A complete internal and external mould of a very small pedicle valve (BB 72373) from loc. 48, colln ASH1, is provisionally assigned to *Gelidorthis*. The valve, which was 2.3 mm long and 3.2 mm

Figs 145–180 *Skenidioides cf. costatus* Cooper, internal moulds of pedicle valves: 145 = BB 72388, $\times 2.5$, 146 = BB 72391, $\times 4.6$, 147 = BB 72390, $\times 5.4$, 148 = BB 72393, $\times 4$, 149 = BB 72389, $\times 3$, 150 = BB 72392, $\times 4.3$; internal and external moulds of brachial valves: 151 = BB 72384a, $\times 3.5$, 152 = BB 72384b, $\times 3.5$, 153 = BB 72383a, $\times 4$, 154 = BB 72383, $\times 4$, 155 = BB 72386, $\times 5$, 156 = BB 72385b, $\times 5.7$, 157 = BB 72385a, $\times 5.7$, 158 = BB 72387b, $\times 3.4$, 159 = BB 72387a, $\times 3.4$. ? *Drabovia* sp., internal mould of brachial valve: 160 = BB 72372, $\times 1.7$. *Destombesium* sp., internal mould of brachial valve: 161 = BB 72375, $\times 2$. *Dalmanella multiplicata multiplicata* (Bancroft), internal and external moulds of brachial valves: 162 = lectotype BB 9379, $\times 1.5$, 163 = BB 72308a, $\times 1.4$, 164 = BB 72308b, $\times 1.5$, 165 = BB 72296b, $\times 1.8$, 166 = BB 72296a, $\times 2$, 167 = BB 72297, $\times 2$, 168 = BB 72295a, $\times 2.1$, 169 = BB 72295b, $\times 2$, 170 = BB 72309, $\times 2$, 178 = BB 72304, $\times 1.3$, 179 = BB 72305a, $\times 2$, 180 = BB 72305b, $\times 1.3$; internal moulds of pedicle valves: 171 = BB 72292, $\times 2$, 172 = BB 72293, $\times 1.8$, 173 = BB 72307, $\times 3$, 174 = BB 72294, $\times 2$, 175 = BB 72306, $\times 2.7$, 176 = BB 72303, $\times 1.8$, 177 = BB 72302, $\times 1.3$.



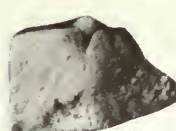
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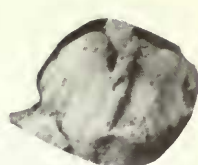
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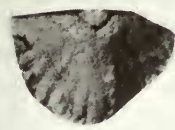
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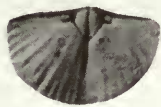
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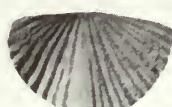
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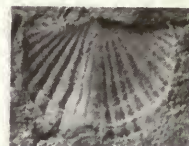
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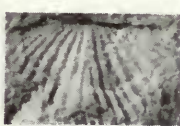
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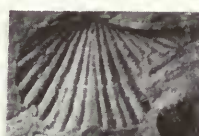
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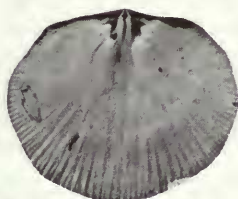
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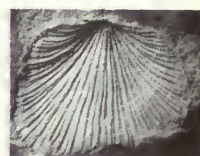
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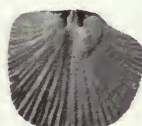
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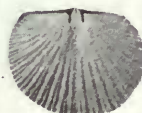
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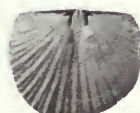
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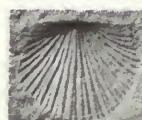
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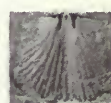
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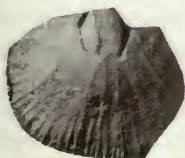
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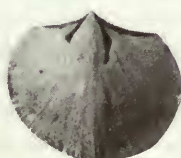
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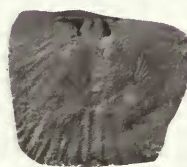
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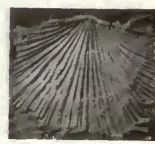
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180

wide, was evenly convex and very shallow. Radial ornamentation of relatively coarse angular ribs; obscure ventral muscle field; dental plates very short and subparallel.

Plectorthid gen. et sp. indet.

Fig. 144

A complete pedicle valve (BB 72374) from loc. 44, colln OA32, is a plectorthid. The subcircular valve was 6·8 mm long, 10·0 mm wide and 2·3 mm deep. The external surface was ornamented by branching hollow costellae. The teeth were small and supported by short, widely-divergent dental lamellae extending anteriorly for 12% of the length of the valve; muscle scar rounded and sub-pentagonal, extending anteriorly for 21% of the length of the valve and 30% as wide as the valve is long.

Family **SKENIDIIDAE** Kozłowski, 1929

Genus **SKENIDIOIDES** Schuchert & Cooper, 1931

Skenidioides cf. *costatus* Cooper

Figs 145–159

- cf. 1956 *Skenidioides* cf. *costatus* Cooper : 493–494; pl. 97, figs 33–48.
 cf. 1962 *Skenidioides* cf. *costatus* Cooper; Williams : 126–127; pl. 11, figs 24–27, 52.
 cf. 1963 *Skenidioides* cf. *costatus* Cooper; Williams : 375–377; pl. 4, figs 7–14.
 cf. 1974 *Skenidioides* cf. *costatus* Cooper; Williams: 82–83; pl. 13, figs 14–16; pl. 14, figs 1–3.

DESCRIPTION. Ventribiconvex, oval *Skenidioides* with a pedicle valve 74% as long as wide and 26% as deep as long; brachial valve very gently convex, 70% as long as wide and with a sharp median sulcus originating at umbo; radial ornamentation costellate with 7 or 8 rounded costae occupying each lateral slope and between 3 and 5 costae per mm, 2 mm anteromedially of the dorsal umbo; internal branching common, external absent.

Ventral interior with free spondylium 26% as deep as the length of the valve.

Dorsal interior with thin ridge-like shaft of cardinal process continuous posteriorly with thin high median septum which is 81% as long as the valve; brachiphore bases converging onto dorsal septum and extending anteriorly for 37% of the valve length and 52% as wide as the valve is long; adductor muscle field impressed about median septum and extending anteriorly for nearly three-quarters of the valve length.

MATERIAL AND LOCALITIES. Loc. 27, colln M2 (e.g. Fig. 147, BB 72390, length 3·8 mm, width 5·0 mm). Loc. 43, colln CP2 (e.g. Fig. 145, BB 72388, length 6·2 mm, width 8·0 mm and Fig. 149, BB 72389). Loc. 44, colln OA29 (e.g. Figs 151–2, BB 72384, length 3·9 mm, width 5·8 mm, and Figs 156–7, BB 72385, length 2·5 mm, width 3·5 mm). Loc. 45, colln AS4 (e.g. Figs 153–4, BB 72383, length 4·0 mm, width 5·2 mm) and colln OA30 (e.g. Fig. 155, BB 72386). Loc. 48, colln ASH1 (e.g. Fig. 148, BB 72393, and Fig. 150, BB 72392, length 3·5 mm, width 5·4 mm) and colln ASH2 (e.g. Figs 158–9, BB 72387, and Fig. 146, BB 72391).

DISCUSSION. *Skenidioides* occurs sporadically throughout the Actonian. Two small samples, one from calcareous sandstones (loc. 48) and the other from siltstones (locs 43–5), have been statistically analysed (see Tables 36–42). They do not differ from each other in bivariate characteristics, or from *S. cf. costatus* (see Williams 1963) found in the Gelli-grin Calcareous Ashes of north Wales. The sample from the siltstone has similar ribbing to *S. cf. costatus* from the Gelli-grin Calcareous Ashes but it may be slightly finer than in the *Skenidioides* from the calcareous sandstones, in which one dorsal valve had only 3 ribs at the fixed distance from the umbo as opposed to 4 or 5. However, this possible difference is not considered important enough to warrant taxonomic recognition and so all *Skenidioides* from the Actonian are recorded as *S. cf. costatus*.

Superfamily **ENTELETACEA** Waagen, 1884
 Family **SCHIZOPHORIIDAE** Schuchert & Le Vene, 1929
 Subfamily **DRABOVIINAE** Havlíček, 1950
 Genus **DESTOMBESIUM** Havlíček, 1970

Destombesium sp.

Fig. 161

An internal mould of a brachial valve (BB 72375) from loc. 25, colln WFT8 is provisionally assigned to *Destombesium*. The subcircular valve was 6.3 mm long and 7 mm wide, with a well-developed median sulcus, and a short, planar, anacline interarea. Valve interior with very thin undifferentiated cardinal process filling narrow notothyrium; brachiophores thin, subparallel and extending anteriorly for 16% of the valve length and splayed laterally for 25% of the valve length; brachiophore bases convergent; fulcral plates present; adductor muscle scars not impressed. Although the single specimen cannot be statistically compared with any described species of the genus, it is similar to *D. zagoraensis* from the Ashgill of Morocco (see Havlíček 1971 : pl. 15).

Genus **DRABOVIA** Havlíček, 1950

? *Drabovia* sp.

Fig. 160

The internal mould (BB 72372) of a brachial valve about 8 mm long and 10 mm wide from the Acton Scott Beds (loc. 46) is questionably assigned to *Drabovia*. The valve is subcircular in outline and about one-quarter as deep as long and with a shallow median sulcus. Interarea short, slightly curved, anacline, cardinal process with small, bulbous, crenulated myophore and long thin shaft; brachiophores short with convergent bases and about one-fifth as long as the valve and splaying laterally for one-quarter the valve width, sockets defined by fulcral plates; muscle scar unknown.

Family **DALMANELLIDAE** Schuchert, 1913

Genus **DALMANELLA** Hall & Clarke, 1892

Dalmanella multiplicata multiplicata (Bancroft)

Figs 162–185

1928a *Wattsella multiplicata* Bancroft : 58–59; pl. 2, figs 11–14.

DESCRIPTION. Typically rounded ventribiconvex *Dalmanella*, with an evenly, weakly convex brachial valve 80% as long as wide and with a very shallow median sulcus; pedicle valve 85% as long as wide and 26% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist inconspicuous, ventral interarea curved apscaline, longer than anacline dorsal interarea; radial ornamentation of costellae commonly 4 to 6 per mm, 2 mm anteromedially of the dorsal umbo; rib branching complex with both external and internal secondaries freely developed except on the first primary which only has internals.

Ventral muscle field bilobed, with diductor scars extending anteriorly for 32% of the length of the pedicle valve but not surrounding the median adductor muscle field; diductor scars 32% as wide as the pedicle valve is long; teeth small, with shallow crural fossettes variably developed, and supported by dental plates, extending anteriorly for 21% of the length of the pedicle valve, along the sides of the diductor muscle area as a pair of strong, slightly convergent ridges.

Dorsal interior with cardinal process consisting of thin linear shaft with small, expanded, rounded myophore which is crenulated; brachiophores short, strong, divergent, with parallel to subparallel bases flanking well-developed notothyrial platform and extending anteriorly for 20% of the length of the brachial valve and splaying laterally for 31% of the valve length; elongately suboval adductor scars poorly differentiated, often obscured by ribbing, situated on either side of low median ridge and extending anteriorly for 50% of the length of the brachial valve.

MATERIAL AND LOCALITIES. Lectotype (selected Cocks 1978 : 62) Fig. 162, BB 9379, length 16.0 mm, width 20.7 mm; also Figs 165–9 and 171, 172, 174, BB 72292–7, all from loc. 18, new material colln x. Figs 176–180, BB 72302–5, from loc. 19, colln CL3. Figs 181–5, BB 72310–3, from loc. 27, colln M1. Figs 163–4, BB 72308, length 13.9 mm, width 16.0 mm; Fig. 170, BB 72309, length 5.8 mm, width 6.3 mm; Fig. 173, BB 72307, length 3.8 mm, width 4.5 mm and Fig. 175, BB 72306, length 5.8 mm, width 7.0 mm; all from loc. 15, colln W8. Also recorded from locs 10–14, 16, 17, 21–3, 26 and 32, all in the Cheney Longville Formation.

DISCUSSION. See p. 248.

Dalmanella multiplicata (Bancroft) *prima* subsp. nov.

Figs 186–190

DESCRIPTION. Like *Dalmanella multiplicata* but with a brachial valve 75% as long as wide; divergent brachiophores with subparallel brachiophore bases 22% as long as the brachial valve and splaying laterally for 36% the length of the valve; dorsal muscle field 53% as long as the brachial valve; pedicle valve 86% as long as wide and 30% as deep as long; dental plates extend anteriorly for 21% of the length of the pedicle valve; ventral muscle field 28% as long as the pedicle valve and 34% as wide as the valve is long; radial ornamentation of costellae commonly 5 per mm, 2 mm anteromedially of the dorsal umbo.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72298, Fig. 190, holotype	3.6	4.3
Internal mould of pedicle valve, BB 72299, Fig. 189	3.5	4.2
Internal mould of brachial valve, BB 72300, Fig. 188	1.9	3.0
External and internal mould of brachial valve, BB 72301a b, Figs 186–7	3.1	4.8

HORIZON AND LOCALITIES. Type material from loc. 3 (colln O60). Also recorded from locs 1, 2, 4–8, all in the Alternata Limestone Formation.

DISCUSSION. See p. 248.

Dalmanella unguis unguis (J. de C. Sowerby)

Figs 200–207

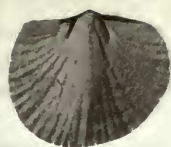
1839 *Terebratula unguis* J. de C. Sowerby in Murchison : 640; pl. 21, fig. 13.

1871 *Orthis unguis* (J. de C. Sowerby) Davidson : 257; pl. 37, figs 16–22.

1945 *Wattsellia unguis* (J. de C. Sowerby) Bancroft : 196–197; pl. 23, figs 8–11; pl. 24, figs 6–7.

1958 *Dalmanella unguis* (J. de C. Sowerby) Dean : pl. 25, fig. 4.

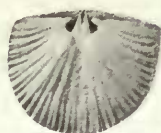
Figs 181–218 *Dalmanella multiplicata multiplicata* (Bancroft), internal moulds of pedicle valves: 181 = BB 72313, $\times 2.5$, 182 = BB 72312, $\times 2.3$; internal and external moulds of brachial valves: 183 = BB 72310a, $\times 2.4$, 184 = BB 72310b, $\times 2.2$, 185 = BB 72311, $\times 2.5$. *Dalmanella multiplicata prima* subsp. nov., internal and external moulds of brachial valves: 186 = BB 72301b, $\times 4.8$, 187 = BB 72301a, $\times 3.8$, 188 = BB 72300, $\times 4.3$; internal moulds of pedicle valves: 189 = BB 72299, $\times 4.5$, 190 = holotype BB 72298, $\times 4.8$. *Dalmanella wattsi* (Bancroft), internal moulds of pedicle valves: 191 = BB 72316, $\times 1.5$, 192 = BB 72315, $\times 1.5$, 193 = BB 72314, $\times 1$; internal and external moulds of brachial valves: 194 = BB 72317b, $\times 1.2$, 195 = BB 72317a, $\times 1.2$, 196 = BB 72318a, $\times 1.4$, 197 = BB 72318b, $\times 1.1$, 198 = BB 72336a, $\times 1.1$, 199 = BB 72336b, $\times 1.3$. *Dalmanella unguis unguis* (J. de C. Sowerby), internal and external moulds of brachial valves: 200 = BB 72322, $\times 2$, 201 = BB 72321, $\times 2$, 202 = BB 72323a, $\times 1.6$, 203 = BB 72323b, $\times 1.4$; internal moulds of pedicle valves: 204 = BB 72319, $\times 1.3$, 205 = BB 72320, $\times 2.3$, 206 = BB 72324, $\times 1.3$, 207 = BB 72325, $\times 1.9$. *Dalmanella unguis ultima* subsp. nov., internal moulds of pedicle valves: 208 = BB 72334, $\times 3.5$, 209 = BB 72328, $\times 2.4$, 210 = BB 72327, $\times 3$, 217 = holotype BB 72326, $\times 4$, 218 = BB 72335, $\times 2$; internal and external moulds of brachial valves: 211 = BB 72332, $\times 5.2$, 212 = BB 72331, $\times 3.2$, 213 = BB 72329, $\times 2$, 214 = BB 72330, $\times 2$, 215 = BB 72333a, $\times 1.7$, 216 = BB 72333b, $\times 1.7$.



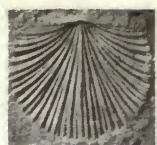
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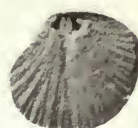
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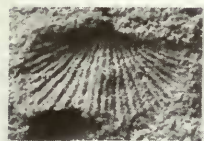
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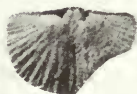
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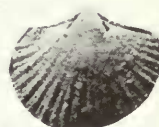
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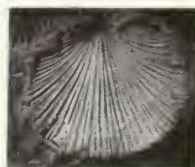
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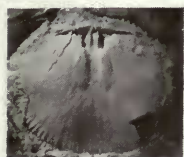
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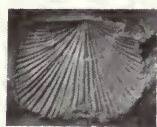
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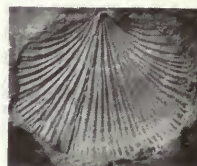
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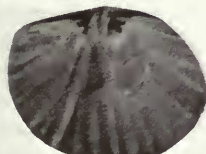
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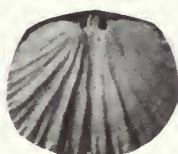
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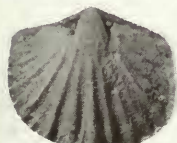
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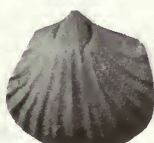
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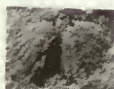
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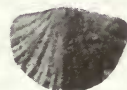
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DESCRIPTION. Large ventribiconvex *Dalmanella* with evenly convex brachial valve 81% as long as wide and with an obscure median sulcus; pedicle valve 87% as long as wide and 32% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist obscure, ventral interarea moderately high, curved apscaline, longer than anacline dorsal interarea; radial ornamentation of very coarse plicae, commonly 2 or 3 ribs per mm, 2 mm anteromedially of the dorsal umbo; branching fairly simple with externals rarely developed.

Ventral muscle field bilobed with diductor muscles extending anteriorly for 39% of the length of the pedicle valve and appearing not to surround the median adductor muscle field; diductor muscle field 30% as wide as the pedicle valve is long; teeth small, stubby, with variably developed crural fossettes and supported by strong dental plates extending anteriorly for 22% the length of the pedicle valve and extending forward as strong convergent ridges bounding the diductor scars.

Dorsal interior with cardinal process consisting of a short, moderately thick linear shaft with expanded, rounded, crenulated single or bilobed myophore; brachiophores short, strong, divergent, with divergent bases flanking poorly-developed notothyrial platform and extending anteriorly for 20% of the length of the brachial valve and splaying laterally for 29% of the valve length; weakly impressed, elongately oval adductor scars poorly differentiated and separated posteriorly by a very low rounded median ridge and extending anteriorly for 49% of the length of the brachial valve; interior of valve often strongly ribbed and obscuring dorsal adductor scar.

MATERIAL AND LOCALITIES. Lectotype (selected Cocks 1978 : 63) GSM Geol. Soc. Colln 6864, from Cheney Longville Flags, 'Horderley' (exact locality unknown). Recorded here from the Crosspipes Member, loc. 27, colln M5 (e.g. Fig. 201, BB 72321, length 7.2 mm, width 8.8 mm; Fig. 204, BB 72319, length 13.2 mm, width 14.9 mm; Fig. 205, BB 72320, length 8.9 mm, width 9.4 mm) and loc. 24, colln WFT1 (e.g. Fig. 200, BB 72322; Figs 202-3, BB 72323; Figs 206-7, BB 72324-5). Also from locs 21, 29, 30 and 33.

DISCUSSION. See p. 248.

Dalmanella unguis (J. de C. Sowerby) *ultima* subsp. nov.

Figs 208-218

DESCRIPTION. Like *Dalmanella unguis* but with a brachial valve 78% as long as wide; divergent brachiophores with slightly divergent brachiophore bases extending anteriorly for 33% of the length of the brachial valve and splaying laterally for 22% of length of valve; dorsal muscle field 54% as long as the brachial valve; pedicle valve 81% as long as wide and 26% as deep as long; dental plates extend anteriorly for 23% of the length of the pedicle valve; ventral muscle scar 35% as long as the pedicle valve and 40% as wide as the valve is long; radial ornamentation of costellae commonly 4 or 5 per mm, 2 mm anteromedially of the dorsal umbo.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72326, holotype	3.1	3.9
Internal mould of pedicle valve, BB 72327	3.7	4.2
Internal mould of pedicle valve, BB 72328	3.5	5.0
Internal mould of brachial valve, BB 72329	5.8	6.6
Internal mould of brachial valve, BB 72330	5.8	6.5
Internal mould of brachial valve, BB 72331	3.0	3.7
Internal mould of brachial valve, BB 72332	1.7	2.2
External and internal moulds of brachial valve, BB 72333a, b	5.4	7.0
Internal mould of pedicle valve, BB 72334	2.8	3.6
Internal mould of pedicle valve, BB 72335	5.3	6.8

HORIZON AND LOCALITIES. BB 72326-31 from loc. 47, colln CF1. BB 72332-5 from loc. 27, colln M8. Also recorded from loc. 21.

DISCUSSION. See p. 248.

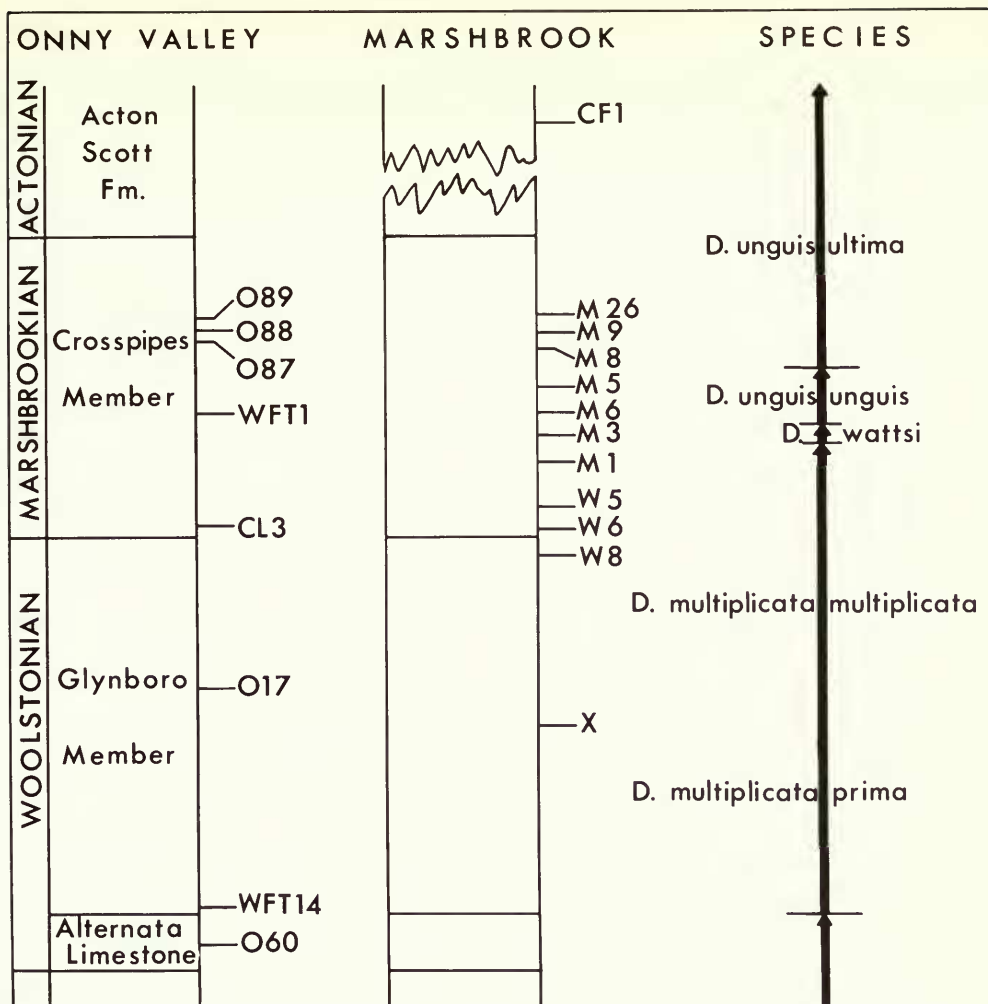


Fig. 219 The stratigraphical location of the *Dalmanella* samples used in the bivariate analysis in the Onny Valley and Marshbrook sections, and the range of the *Dalmanella* species and subspecies.

Dalmanella wattsii (Bancroft)

Figs 191–199

1928a *Wattsella wattsii* Bancroft : 58; pl. 1, figs 1–5.

1945 *Wattsella wattsii* Bancroft : 195–196; pl. 23, fig. 7; pl. 24, figs 2–5.

1958 *Dalmanella wattsii* (Bancroft) Dean : pl. 25, figs 2–3.

1963 *Dalmanella wattsii* (Bancroft); Williams & Wright : pl. 1, figs 2, 6, 9; pl. 2, fig. 3.

DESCRIPTION. Large ventribiconvex *Dalmanella* with an evenly, feebly convex brachial valve 82% as long as wide and with a shallow, often obscure median sulcus; pedicle valve 85% as long as wide and 23% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist inconspicuous, ventral interarea moderately high, curved apscaline, longer than anacline dorsal interarea; radial ornamentation of coarse costellae, 3 or 4 per mm, 2 mm anteromedially of the dorsal umbo; branching complex, both externals and internals freely developed except on the first primary, which only has internals.

Ventral muscle field bilobed, with diductor muscles extending anteriorly for 38% of the length of the pedicle valve but not surrounding the median elongately oval adductor muscle field;

diductor muscle field 28% as wide as the pedicle valve is long; teeth small with variably developed shallow crural fossettes, and supported by strong dental plates extending anteriorly for 18% of the length of the pedicle valve and extending forward as strong, slightly convergent ridges bounding the diductor scars.

Dorsal interior with cardinal process consisting of strong, rounded shaft with expanded single or bilobed crenulated myophore extending slightly beyond the hinge; brachioophores very short, strongly divergent, with parallel bases flanking very well developed notothyrial platform and extending anteriorly for 18% of the length of the brachial valve, and splaying laterally for 30% of the valve length; weakly-impressed elongately oval adductor scars poorly differentiated, situated on either side of low, rounded median ridge and extending anteriorly for 45% of the length of the brachial valve.

MATERIAL AND LOCALITIES. Lectotype (selected Cocks 1978 : 63) BB 73833, from loc. 27, from which came colln M3, including Fig. 191, BB 72316, length 15.5 mm, width 19.4 mm; Fig. 192, BB 72315, length 17.0 mm, width 19.0 mm; Fig. 193, BB 72314, length 16.8 mm, width 22.0 mm; Figs 194–5, BB 72317, length 14.0 mm, width 17.0 mm; Figs 196–7, BB 72318, length 13.2 mm, width 15.2 mm; Figs 198–9, BB 72336, length 14.5 mm, width 18.4 mm. Other specimens from loc. 31, also in the Crosspipes Member.

DISCUSSION. *Dalmanella* occurs sporadically throughout the Alternata Limestone Formation and Glynboro Member, but is particularly abundant in the uppermost part of the Glynboro Member and the Crosspipes Member. The calcareous sandstone Henley Member within the Acton Scott Formation at Acton Scott also yields a *Dalmanella*. Fig. 219 shows the stratigraphical positions, in two separate sections in the Caradoc district, of the samples used to derive the statistics given in Tables 43–53. The overwhelming abundance of *Dalmanella* populations precludes a bed-by-bed bivariate analysis. The sampling interval chosen for statistical analysis of the populations was primarily dictated by outcrop availability, but where sedimentary facies changes occurred, a close sampling interval was employed. A qualitative assessment of *Dalmanella* populations was made between each measured collection.

Only one measurable population of *Dalmanella multiplicata prima* subsp. nov. (colln O60, loc. 63) was available from the Alternata Limestone, and this differed significantly from the stratigraphically younger colln WFT14 (loc. 14), in having a brachial valve which increased in width faster ($P < 0.01$) and in its longer ventral muscle scar ($P < 0.05$). Further, the O60 population differs significantly from the topotype *D. multiplicata multiplicata* (Bancroft) population (colln x; loc. 18), in having a brachial valve which increased in width faster ($P < 0.01$) and in faster growth in relative depth of the pedicle valve ($P < 0.02$). In other respects, including ribbing (Table 53), the new subspecies closely resembles *D. multiplicata multiplicata*. In view of these morphological differences only a new subspecies has been recognized, so as to emphasize the close relationship with *D. multiplicata multiplicata*. The new subspecies appears to be limited to the Alternata Limestone.

The upper Glynboro Member and the lower part of the Crosspipes Member (up to and including the *Dalmanella watsi* Zone of Bancroft 1929a, b, 1933) contain abundant *Dalmanella* populations with much morphological variation. The *D. multiplicata multiplicata* topotype population (colln x) differs significantly from the W8 population in having relatively narrower dorsal cardinalia ($P < 0.05$) and faster increase in relative length of the ventral muscle field. The W8 population does not differ from the W6 population with respect to any character, and in turn the W6 population does not differ from the W5 population nor from the M1 population (see Fig. 219).

Dalmanella population CL3 does not differ in any character from population W5, and only differs from the older population O17 in having relatively wider dorsal cardinalia ($P < 0.05$). The O17 population does not differ in any character from the WFT14 population, which in turn differs solely from the topotype population of *D. multiplicata multiplicata* in having relatively wider dorsal cardinalia ($P < 0.05$).

In view of the non-directional but persistent morphological variation expressed by *Dalmanella* populations in the Glynboro and lower Crosspipes Members (to the top of the *D. watsi* Zone of Bancroft 1929a, b, 1933), in both sections, it is proposed to include all the populations present in

the one subspecies, *D. multiplicata multiplicata* (Bancroft). This is supported by the limited data on ribbing (Table 53), which show that there is no significant difference in ribbing densities of the *D. multiplicata* topotype population and the younger population (M1) of the same species.

Bancroft (1928a, 1945) gave the type locality for *Dalmanella watsi*, in the old quarry in Marshwood (loc. 27), in the *Heterorthis praeculta* beds, 3 in (76 mm) below the base of the 'Wattsella' *unguis* beds. The topotype population (collection M3) differs significantly from the stratigraphically older M1 population on four counts, the relatively wider brachial valve ($P < 0.05$), the slower increase in length of the dorsal cardinalia ($P < 0.05$), the relatively longer pedicle valve ($P < 0.05$) and the slower increase in ventral muscle field width ($P < 0.01$). The fact that the brachial valve is significantly wider and the pedicle valve significantly longer probably reflects that the pedicle interarea of *D. watsi* is longer than that of the M1 population and as such the increase in posterior growth of the interarea is greater relative to the increase in valve width. Further, in *D. watsi* the ribbing is significantly coarser ($P < 0.001$) than the M1 population of *D. multiplicata multiplicata*.

The topotype population of *D. watsi* does not differ from the topotype *D. multiplicata multiplicata* in bivariate characters, but their ribbing is different. In *D. watsi* the ribbing is significantly coarser ($P < 0.001$). Bancroft (1928a) maintained that *D. watsi* could be differentiated on a series of costellae insertions (Table 11). However, the only significant difference is the earlier insertion of 4a relative to 4b in *D. watsi*. *D. watsi* has only been found in the Marshbrook area (locs 27 and 31).

The topotype population (colln M6; loc. 27) of *D. unguis* differs from *D. watsi* in the faster increase in length of the dorsal cardinalia ($P < 0.01$), the relatively wider pedicle valve ($P < 0.05$), the slower growth in relative depth of the pedicle valve ($P < 0.05$) and the wider ventral muscle scar ($P < 0.05$). *D. unguis* (colls M5 and M6 pooled) has significantly coarser ribbing ($P < 0.05$). From the topotype population of *D. multiplicata multiplicata*, *D. unguis* differs in having significantly coarser ribbing ($P < 0.001$), faster increase in length of the dorsal cardinalia ($P < 0.02$) and slower growth in relative depth of the pedicle valve ($P < 0.001$).

The *Dalmanella* populations present in the upper part (*D. unguis* and *O. reuschi* Zones of Bancroft 1929a, b) of the Crosspipes Member also display a great deal of morphological variability. Population M5, which occurs stratigraphically above the topotype *D. unguis* population, differs in having relatively longer dorsal cardinalia ($P < 0.01$) and faster growth in relative depth of the pedicle valve. There is no ribbing difference.

There is no significant bivariate character difference between *Dalmanella* populations M5–M8, M8–M9 and M9–M26. Population WFTI differs from the topotype of *D. unguis* in having relatively shorter dorsal cardinalia ($P < 0.01$) and in the faster increase in length of the dorsal adductor muscle field. Further, the WFTI population does not differ, as regards bivariate characters, from the stratigraphically younger O87–89 population. However, this latter population differs from the youngest population in the Marshbrook section (M26) in the faster increase in relative width of the brachial valve ($P < 0.01$).

Thus the *Dalmanella* populations of the Upper Cheney Longville Formation show no consistent morphological variation. However, the populations in the upper part of the *D. unguis* Zone, in both sections, show a consistent difference from the older populations, in having finer ribs (Table 53). The M6, M5 and WFTI populations do not differ significantly as regards coarseness of ribbing. However, the younger populations of M8–M9 (pooled data) differ from M6, M5 and WFTI (all at $P < 0.001$), whilst O87–89 differs from the same collections ($P < 0.01$). This consistent morphological difference is afforded taxonomic recognition, with the erection of the subspecies *D. unguis ultima* to cover forms with a modal rib count of 4 or 5 per mm, at 2 mm anteromedially from the dorsal umbo, as opposed to the 2 or 3 of *D. unguis unguis*.

In calcareous bioturbated sandstones of the stratigraphically younger Acton Scott Formation *D. unguis ultima* briefly reappears (loc. 47). The population CF1 does not differ from the previous populations of the subspecies, in either bivariate statistics or ribbing.

Dean (1958 : 205) reported sympatry between *D. watsi* and *D. unguis*, at least in the Marshbrook area. This is contrary to the findings here. Large collections of basal *D. unguis* Zone specimens show a wide range of continuous morphological variation especially with respect to

ribbing, which is the easiest qualitative character by which to distinguish the two species. Presumably Dean would place the finer-ribbed specimens in *D. wattsi*, but this would involve splitting a continuous morphological series into two categories and would be unjustified.

Genus *BANCROFTINA* Sinclair, 1946

- 1933 *Raymondella* Bancroft : 3 (*nomen nudum*).
 1938 *Raymondella* Bancroft; Whittington : 249 (*non* Reed 1935 : 8).
 1945 *Raymondella* Bancroft : 197.
 1946 *Bancroftina* Sinclair : 295.

DIAGNOSIS (emended). Subcircular to subquadrate ventribiconvex shells with shallow sulcate brachial valve; radial ornamentation finely costellate with first order costellae branching internally, more commonly than externally, in the first four sectors. Ventral interarea moderately long, curved and apscaline with open delthyrium; dorsal interarea short, weakly curved, anacline, notothyrium open and commonly filled with cardinal process; shell punctate.

Ventral interior with massive teeth supported by well-developed subparallel to divergent dental lamellae; muscle field subtriangular to bilobed in outline with submedian diductor lobes not enclosing median adductor scar; pedicle callist well developed; pallial sinus pattern unknown.

Dorsal interior with stout bilobed or trilobed cardinal process; brachiophores very stout and short, widely divergent with their bases greatly divergent relative to their tops and often subparallel to hinge line; fulcral plates rarely developed; ancillary struts often strong, fused to well-developed median ridge; dorsal adductor scar elongately oval and bipartite or quadripartite.

TYPE SPECIES. *Raymondella typa* Whittington, by original definition of Sinclair (1946 : 295).

DISCUSSION. Bancroft (1933 : 3) initially proposed the name *Raymondella*, with *R. typa* as genotype, for a group of middle Caradoc dalmanellid brachiopods from the upper Horderley Sandstone, Alternata Limestone and lower Longville Flags (all Longvillian) of the type Caradoc. The diagnosis was inadequate and most subsequent workers (see Williams & Wright 1963 : 27) have treated this as a *nomen nudum*. However, Whittington (1938 : 249) fully described *Raymondella typa*, based on composite material including specimens of his own from silty ashes of the Berwyn Dome and the material Bancroft had at his disposal. Whittington attributed the genus and the species to Bancroft. *Raymondella* was further described by Bancroft (1945) but as the authorship of the genus has to be attributed to the first full description of Whittington (1938), the name was by that time occupied (Reed 1935). Thus Sinclair (1946, 1949) proposed the name *Bancroftina* to cover the Caradoc dalmanellid and designated *Raymondella typa* Whittington as the type species.

Bancroftina hewitti sp. nov.

Figs 247–250

DESCRIPTION. Large subcircular, unequally biconvex *Bancroftina*, with shallow sulcate brachial valve 79% as long as wide and less than one-tenth as deep as long, and pedicle valve 80% as long as wide and 28% as deep as long; radial ornamentation moderately coarsely costellate with a modal count of 4 costellae per mm, 2 mm anterior of the dorsal umbo, external branching earlier

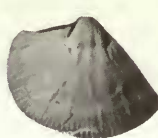
Figs 220–246 *Bancroftina whittingtoni* sp. nov., internal moulds of pedicle valves: 220 = BU 241, $\times 1.8$, 221 = BB 73681, $\times 2$, 222 = BB 72469, $\times 1.5$, 223 = BB 73677, $\times 1.7$, 224 = BB 73678, $\times 1.9$, 225 = BB 72467, $\times 2$, 226 = BB 72468, $\times 1.8$; internal and external moulds of brachial valves: 227 = holotype BB 72475, $\times 1.8$, 228 = BB 72476, $\times 1.9$, 229 = BB 72472, $\times 1.9$, 230 = BB 72473, $\times 1.9$, 231 = BB 72471, $\times 1.7$, 232 = BB 72474, $\times 1.7$, 233 = BB 72470, $\times 1.9$. *Bancroftina typa* (Whittington), internal moulds of pedicle valves: 234 = BB 72480, $\times 2$, 235 = BB 72481, $\times 2$, 244 = BB 72479, $\times 1.3$, 245 = BB 72486, $\times 1.1$, 246 = BB 72487, $\times 1.6$; internal and external moulds of brachial valves: 236 = BB 72483, $\times 2$, 237 = BB 72482, $\times 2$, 238 = lectotype BU 242, $\times 1.8$, 239 = lectotype of *robusta* BB 10302, $\times 2.5$, 240 = BB 72484, $\times 1.8$, 241 = BB 72477, $\times 1.9$, 242 = BB 72478, $\times 1.5$, 243 = BB 72485, $\times 1.7$.



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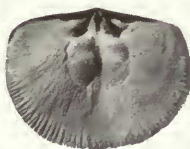
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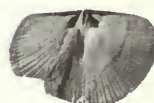
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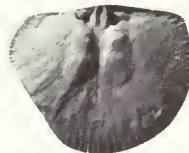
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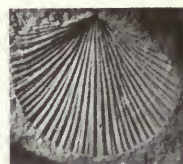
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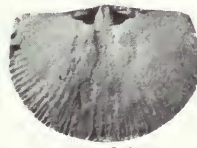
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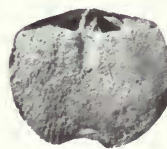
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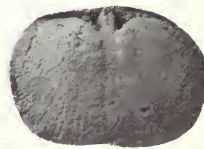
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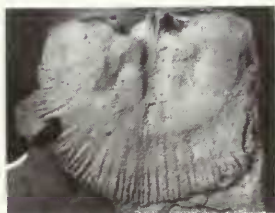
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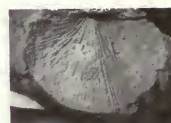
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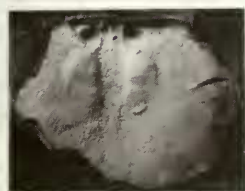
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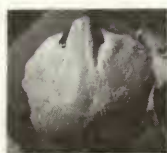
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246

than internal slightly more common in sectors I to IV; dental lamellae very strong, weakly divergent and extending anteriorly for 17% of the length of the valve, crural fossettes absent, ventral muscle scar extending anteriorly for 35% of the length of the valve and 30% as wide as the valve is long; heavily calcified cardinalia with divergent brachiophore bases 14% the length of the brachial valve and 27% as wide as the valve is long; ancillary struts massive, ankylosed to median ridge, bipartite dorsal adductor scar extending anteriorly for 42% the length of the valve.

NAME. After Dr R. A. Hewitt.

DIMENSIONS.	length	width
Internal mould of brachial valve, BB 72488, holotype	19.3	23.0
Internal mould of pedicle valve, BB 72489	16.7	18.6
Internal mould of brachial valve, BB 72490	16.7	20.1
Internal mould of pedicle valve, BB 72491	18.3	23.6

HORIZON AND LOCALITIES. All figured specimens from loc. 32; holotype BB 72488, colln LM4, remainder colln LM6. Also recorded from locs 26 and 27.

DISCUSSION. See p. 253.

Bancroftina typa (Whittington)

Figs 234–246

- 1933 *Raymondella typa* Bancroft : 3; *nomen nudum*.
 1938 *Raymondella typa* Bancroft; Whittington : 249 *pars*; pl. 10, fig. 13, *non* figs 12, 14.
 1945 *Raymondella typa* Bancroft; Bancroft : 198–201; pl. 25, figs 1–10.
 1945 *Raymondella robusta* Bancroft : 201; pl. 25, figs 11, 12; pl. 26, figs 1–3.
 1946 *Bancroftina typa* (Bancroft) Sinclair : 295.
 1959 *Bancroftina typa* (Whittington); Cave & Dean : 294; pl. 53, figs 5, 6.
 1963 *Bancroftina typa* (Whittington); Williams & Wright : 7; pl. 1, figs 12, 15; pl. 2, fig. 6.
 1963 *Bancroftina robusta* (Bancroft) Williams & Wright : pl. 1, fig. 13.

DESCRIPTION. Subcircular to subquadrate, unequally biconvex *Bancroftina*, with shallow sulcate brachial valve 79% as long as wide and less than one-eighth as deep as long, and pedicle valve 87% as long as wide and 30% as deep as long; radial ornamentation finely costellate with a modal count of 5 costellae per mm, 2 mm anterior of dorsal umbo, external branching very rarely occurring earlier than internal in sectors I to IV; dental lamellae strongly developed, divergent and extending anteriorly for 21% of the length of the valve, with moderately strong crural fossettes; ventral muscle scar extending anteriorly for 35% of the length of the valve and 32% as wide as the valve is long; strong cardinalia with widely divergent brachiophore bases 19% the length of the brachial valve and 34% as wide as the valve is long; bipartite dorsal adductor scar extending anteriorly for 50% the length of the valve.

MATERIAL AND LOCALITIES. Lectotype (Fig. 238) BU 242 (selected Cave & Dean 1959 : 295), length 10.7 mm, width 14.7 mm, from small quarry in upper Horderley Sandstone at New House, grid ref. SO 418859, from which also came BB 72480 (Fig. 234), length 10.1 mm, width 11.7 mm; BB 72481 (Fig. 235), length 9.7 mm, width 10.4 mm; BB 72482 (Fig. 237), length 9.5 mm, width 10.6 mm; BB 72483 (Fig. 236), length 9.5 mm, width 13.2 mm. From loc. 14, colln WFT19, e.g. BB 72477 (Fig. 241), length 12.4 mm, width 15.2 mm; BB 72478 (Fig. 242), length 9.7 mm, width 13.0 mm; BB 72479 (Fig. 244), length 13.8 mm, width 16.4 mm. From loc. 19, e.g. BB 10302 (Fig. 239), lectotype of *robusta*, length 13.6 mm, width 17.6 mm. From loc. 17, colln S9, e.g. BB 72484–7 (Figs 240, 243, 245–6). Also from locs 1–8, 10 and 16.

Bancroftina whittingtoni sp. nov.

Figs 220–233

- 1938 *Raymondella typa* Bancroft; Whittington : 249 *pars*; pl. 10, figs 12, 14, *non* fig. 13.

DESCRIPTION. Semicircular to subquadrate, unequally biconvex *Bancroftina*, with shallow sulcate

brachial valve 77% as long as wide and less than one-eighth as deep as long, and pedicle valve 81% as long as wide and 34% as deep as long; radial ornamentation very finely costellate with modal count of 7 costellae per mm, 2 mm anterior of dorsal umbo; in sectors I to IV internal branching occurs earlier than external branching; dental lamellae strongly developed, sub-parallel to slightly divergent, and extending anteriorly for 20% of the length of the valve, ventral muscle scar extending anteriorly for 32% of the length of the valve and 31% as wide as the valve is long; strong cardinalia with widely divergent brachiophore bases extending anteriorly for 20% the length of the brachial valve and 32% as wide as the valve is long; dorsal adductor scar extending anteriorly for 53% the length of the valve.

NAME. After Professor H. B. Whittington.

DIMENSIONS.	length	width
Internal mould of brachial valve, BB 72475, holotype	12.3	13.8
Internal mould of pedicle valve, BB 73678	10.5	13.2
Internal mould of pedicle valve, BU 241	13.2	15.2
Internal mould of pedicle valve, BB 73677	10.8	12.5
Internal mould of pedicle valve, BB 72467	9.5	10.6
Internal mould of pedicle valve, BB 72468	7.5	8.0
Internal mould of pedicle valve, BB 72469	12.6	16.0
External mould of brachial valve, BB 72470	9.9	12.2
Internal mould of brachial valve, BB 72471	14.3	17.2
Internal mould of brachial valve, BB 72472	7.5	10.7
Internal mould of brachial valve, BB 72473	12.9	15.2
Internal mould of brachial valve, BB 72474	12.7	14.8

HORIZON AND LOCALITIES. This species is known only from the type beds in the Berwyn Hills (Whittington 1938). The sample used in this study comes from a disused quarry in the Bryngwyn Beds, 360 m north-east of the spot height in the ancient camp at Bryngwyn Hill, some 4.8 km south-west of Llansantffraid; SJ 188184.

DISCUSSION. *Bancroftina* is very abundant in the upper Horderley Sandstone, Alternata Limestone and lower Cheney Longville Formation. Bancroft (1945) recognized *Bancroftina typa* (Whittington) from the Horderley Sandstone and erected a new species *B. robusta*, from the lower Cheney Longville Formation. Previously, Bancroft (1933 : table adjacent to p. 4) had referred to an undescribed species of *Bancroftina*, *B. gigantea* (a *nomen nudum*), as characterizing 165 ft (50 m) of strata, in east Shropshire (Salop), above his *Kjaerina bipartita* Zone (= Alternata Limestone). The type locality of *B. robusta* falls within his zone of *B. gigantea*, suggesting that he was in fact referring to the same species.

The statistical data derived in Tables 54–64 are based on collections which Whittington described as *B. typa* from the Berwyn Hills, *B. typa* from the Horderley Sandstone and *B. robusta*. As Bancroft (1945 : 201) emphasized the importance of size in the species classification of this genus, populations with the largest and smallest individuals and a population from the Alternata Limestone and upper Cheney Longville Formation have also been statistically analysed.

As regards bivariate statistics, *Bancroftina* from the Horderley Sandstone, Alternata Limestone and Glynboro Member, including *B. typa* and *B. robusta* topotypes, do not differ significantly. *Bancroftina* from the Berwyn Hills, north Powys, differs consistently from the above populations in having a slower relative increase in width of the dorsal cardinalia ($P < 0.05$ – 0.001) and relatively longer dorsal cardinalia ($P < 0.05$ – 0.01) and so a new species, *B. whittingtoni*, is described here. *B. hewitti* does not differ significantly from the older populations of *Bancroftina* from Salop but does differ significantly from the Berwyn Hills *Bancroftina* in having relatively shorter dental lamellae ($P < 0.05$).

B. whittingtoni from the Berwyn Hills has significantly finer ribbing (see Table 64) than *B. hewitti* ($P < 0.001$) and the remaining *Bancroftina* populations ($P < 0.01$). *B. hewitti* differs significantly ($P < 0.01$) from the other Salop populations in having the coarsest costellae.

The earlier insertion of eight costellae relative to eight others has been analysed (see Table 63). 1b)1a, 2b)2a, 3a1a)2a, 3a1)3b1 and 4b)4b are constantly associated throughout the seven populations of the three species. 2a1)2b is very variable, forming no consistent patterns. *B. hewitti* differs significantly from the other species in the earlier insertion of 3a relative to 3a1a ($P < 0.001$) and 3a relative to 3c ($P < 0.001$). These two rib patterns are constantly associated in *B. typa* and *B. whittingtoni*.

To summarize, there are three species of *Bancroftina* in the Caradoc of Wales and the Welsh Borderland:

1. *B. whittingtoni* from the Berwyn Hills, which differs from *B. typa* in the configuration of the dorsal cardinalia and in having finer ribbing. From *B. hewitti* it differs in its finer ribbing and dental lamellae.

2. *B. typa*, which includes populations from the Horderley Sandstone originally assigned by Bancroft to *B. robusta*.

3. *B. hewitti*, which is characterized by its coarse ribbing and the costellae insertions 3c)3a and 3a1a)3a. Further, the species has very heavily calcified dorsal cardinalia with secondary calcite deposition around the brachiophores forming large blocks. Its ancillary struts are very strong and in the pedicle valve it does not possess crural fossettes as do *B. whittingtoni* and *B. typa*.

Genus *CRYPTOTHYRIS* Bancroft, 1945

DIAGNOSIS (emended). Subcircular, unequally biconvex dalmanellid with a deeply convex pedicle valve and sulcate brachial valve; radial ornamentation multicostellate; ventral interarea moderately long, curved, apscaline with open delthyrium and prominent umbo; dorsal interarea short and curved, anacline, notothyrium filled by cardinal process; shell punctate.

Ventral interior with massive teeth supported by strong subparallel dental plates with strong crural fossettes on their medial faces, pedicle callist well developed, muscle field subtriangular to cordate in outline, submedian diductor lobes extending beyond dental lamellae and not surrounding anterior edge of median adductor field.

Dorsal interior with stout, undifferentiated, bilobed and anteriorly crenulated cardinal process, brachiophores with massive triangular pads and with their bases slightly divergent relative to their tops, fulcral plates rarely developed; dorsal adductor scar elongate and impressed, quadripartite about strong median ridge.

DISCUSSION. Bancroft (1928a, 1945) and more recently Kemežys (1968) noted that *Cryptothyris* had rhipidomelloid ribbing. However, in internal features this genus belongs unequivocally in the Dalmanellidae, an assignment made in 1965 by Williams *et al.*

TYPE SPECIES. *Resserella paracyclica* Bancroft, 1928.

Figs 247–275 *Bancroftina hewitti* sp. nov., internal moulds of pedicle valves: 247 = BB 72491, $\times 1.2$, 248 = BB 72489, $\times 1.2$; internal moulds of brachial valves: 249 = **holotype** BB 72488, $\times 1.4$, 250 = BB 72490, $\times 1.2$. *Cryptothyris paracyclica* (Bancroft), internal moulds of brachial valves: 251 = lectotype BB 24172, $\times 2.5$, 252 = BB 72502, $\times 1.9$, 253 = BB 73564, $\times 2.4$, 254 = BB 24184, $\times 1.7$, 255 = BB 24180, $\times 1.6$, 256 = BB 72499, $\times 2.2$, 257 = BB 72498, $\times 2$; external surface of brachial valve: 258 = BB 72500, $\times 2.5$; internal moulds of pedicle valves: 260 = BB 24220, $\times 2$, 261 = BB 24221, $\times 2$, 262 = BB 72501, $\times 1.5$, 263 = BB 24216, $\times 2$, 264 = BB 24222, $\times 1.1$, 265 = BB 72496, $\times 1.6$, 266 = BB 72497, $\times 1.6$; external surface of pedicle valve and lectotype of synonymized *C. cyclica*: 259 = BB 24218, $\times 2.5$. *Onniella avelinei* Bancroft, internal mould of brachial valve: 267 = lectotype, BB 10326, $\times 2$. *Onniella reuschi* Bancroft, internal and external moulds of brachial valves: 268 = BB 72414, $\times 1.7$, 269 = BB 72415, $\times 1.8$, 270 = BB 72412, $\times 1.5$, 271 = BB 72413, $\times 1.4$, 272 = BB 72422, $\times 2$, 273 = BB 72420, $\times 2.5$, 274 = BB 10248 (lectotype of synonymized *O. aspasia*), $\times 3$, 275 = BB 72423, $\times 1.9$.



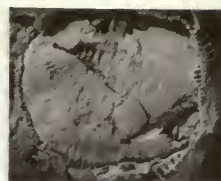
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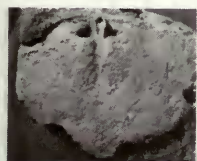
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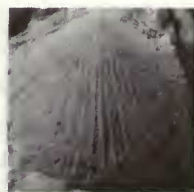
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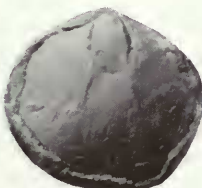
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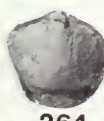
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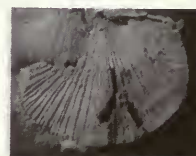
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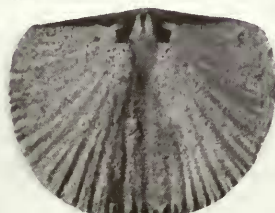
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Cryptothyris paracyclica (Bancroft)

Figs 251–266

1928a *Resserella paracyclica* Bancroft : 56; pl. 1, figs 6–9.1928a *Resserella cyclica* Bancroft : 56; pl. 1, fig. 10.1945 *Cryptothyris paracyclica* (Bancroft) Bancroft : 223.1958 *Cryptothyris paracyclica* (Bancroft); Dean : pl. 25, fig. 7.1963 *Cryptothyris paracyclica* (Bancroft); Williams & Wright : pl. 2, figs 9, 14, 15.

DESCRIPTION (emended). Subcircular, unequally biconvex *Cryptothyris*, with evenly convex brachial valve 80% as long as wide, and pedicle valve 82% as long as wide and 30% as deep as long; radial ornamentation finely costellate with modal count of 4 costellae per mm, 2 mm anteromedially of the dorsal umbo, median costellae commonly developed; subparallel dental lamellae 20% as long as pedicle valve, ventral muscle scar extending anteriorly for 36% the length of the valve and 32% as wide as the valve is long; cardinalia massive with very slightly divergent brachiophore bases extending anteriorly for 19% the length of the valve and splaying laterally for 31% of the valve length; dorsal adductor scar extending anteriorly for 54% of the length of the valve.

MATERIAL AND LOCALITIES. Lectotype (Fig. 251) BB 24172 (selected Cocks 1978 : 64), length 9.2 mm, width 11.3 mm; lectotype of *cyclica* (Fig. 259) BB 24218, length 9.2 mm, width 9.6 mm; also Fig. 253, BB 73564, length 7.1 mm, width 9.4 mm; Fig. 254, BB 24184, length 10.0 mm, width 11.7 mm; Fig. 255, BB 24180, length 9.7 mm, width 11.2 mm; Fig. 257, BB 72498, length 11.1 mm, width 13.0 mm; Fig. 258, BB 72500, length 5.6 mm, width 6.9 mm; Fig. 260, BB 24220, length 8.5 mm, width 9.6 mm; Fig. 261, BB 24221, length 8.9 mm, width 11.0 mm; Fig. 263, BB 24216, length 12.0 mm, width 14.3 mm; Fig. 264, BB 24222, length 10.9 mm, width 12.0 mm; all from loc. 39. Also loc. 44, colln OA1 (e.g. Figs 256, 265–6, BB 72499, BB 72496–7), loc. 43, colln CP2 (e.g. Fig. 252, BB 72502, and Fig. 262, BB 72501). Also recorded from locs 40–2, 45 and 48, all from the Acton Scott Formation.

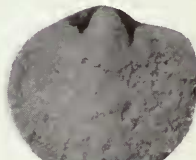
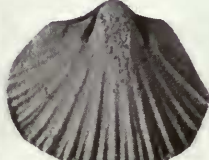
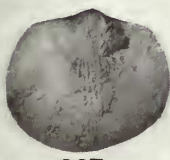
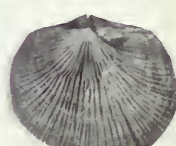
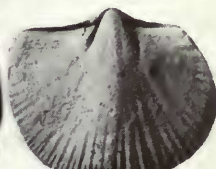
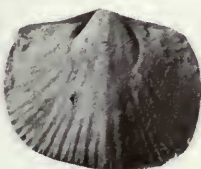
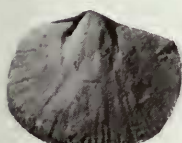
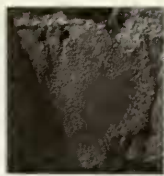
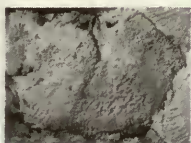
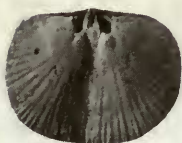
DISCUSSION. Bancroft (1928a, 1945) erected *Resserella paracyclica* and *R. cyclica*, which he later transferred to *Cryptothyris*, from the same type locality in the Acton Scott Formation of the Onny Valley, and distinguished between them by the width of the hinge line. At the type locality *Cryptothyris* is very rare, but from a study of the small amount of Bancroft material in the BM(NH) it is apparent that, as regards hinge width, there is continuous variation between the two species and thus *C. cyclica* is treated as being synonymous with *C. paracyclica*. At loc. 44 in the Acton Scott Formation of Marshbrook a small collection of *C. paracyclica* has been statistically analysed to give some idea of the variation of the species involved (see Tables 65–73).

Genus *ONNIELLA* Bancroft, 1928*Onniella broeggeri* Bancroft

Figs 316–335

1928a *Onniella bröggeri* Bancroft : 56–57; pl. 2, figs 1–5.1945 *Onniella bröggeri* Bancroft; Bancroft : 222–223; pl. 30, figs 16–17.

Figs 276–305 *Onniella reuschi* Bancroft, internal moulds of brachial valves: 276 = BB 72425, $\times 2$, 277 = BB 72424, $\times 2.4$, 278 = BB 72431, $\times 1.5$, 279 = BB 72432, $\times 1.7$; internal moulds of pedicle valves: 280 = BB 72417, $\times 1.8$, 281 = BB 10239 (lectotype of synonymized *O. grandis*), $\times 2$, 282 = BB 72411, $\times 2.4$, 283 = BB 72408, $\times 1.7$, 284 = BB 72410, $\times 1.8$, 285 = BB 72418, $\times 2$, 286 = BB 72421, $\times 2$, 287 = BB 72419, $\times 2.2$, 288 = BB 72428, $\times 1.7$, 289 = BB 72427, $\times 2.5$, 290 = BB 72426, $\times 3$, 291 = BB 72430, $\times 1.7$, 292 = BB 72429, $\times 2.9$, 293 = BB 72409, $\times 1.7$. *Onniella depressa* Bancroft, conjoined valves: 294 = brachial view of BB 10254 (lectotype of synonymized *O. sinuata*), $\times 1.5$, 295 = pedicle view of BB 10254, $\times 1.5$, 296 = brachial view of lectotype BB 10251, $\times 1.5$, 297 = pedicle view of lectotype BB 10251, $\times 1.5$; internal moulds of pedicle valves, 298 = BB 72435, $\times 4$, 299 = BB 72466, $\times 4$, 300 = BB 72434, $\times 2.5$, 301 = BB 72444, $\times 2.5$, 302 = BB 72433, $\times 2.5$, 303 = BB 73679, $\times 2.5$, 304 = BB 72443, $\times 2.5$, 305 = BB 72441, $\times 2.5$.



- 1945 *Onniella inconstans* Bancroft : 221–222; pl. 31, figs 1–3.
 1958 *Onniella inconstans* Bancroft; Dean : pl. 25, figs 8–9.
 1958 *Onniella broeggeri* Bancroft; Dean : pl. 25, figs 10–11.
 1965 *Onniella broeggeri* Bancroft; Cave : pl. 12, figs F, I, L, O, P.

DESCRIPTION (emended). Subquadrate, unequally biconvex *Onniella*, with evenly convex, sulcate brachial valve 76% as long as wide, and pedicle valve 82% as long as wide and 28% as deep as long; shell with right-angular cardinal extremities; dorsal interarea short, curved, anacline, notothyrium open; ventral interarea moderately long, curved apscaline, delthyrium open; radial ornamentation commonly 6 costellae per mm, 2 mm anterior of dorsal umbo, branching freely developed.

Ventral interior with massive stout teeth supported by subparallel to parallel dental lamellae, which extend anteriorly for 22% of the length of the valve, and have moderately strong to very strong crural fossettes on their inner faces; dental plates continued along sides of diductor muscle field as a pair of strong ridges; adult ventral muscle field angular subpentagonal and extending anteriorly for 34% of length of the pedicle valve, maximum width 30% of the valve length; diductor scars elongately oval and produced as short lobes in front of median lanceolate adductors, but not surrounding them.

Dorsal interior with massively calcified cardinalia 21% as long as the brachial valve and 34% as wide as the valve length; brachioophores widely divergent and with weakly divergent bases which are often masked by thick secondary shell deposition to form thick triangular pads ankylosed to median ridge by thick ancillary struts in the form of a straight bar; inner faces of brachioophores with pits; cardinal process with thick shaft continuous with posterior end of median ridge, myophore bilobed and posteriorly crenulated, filling notothyrium and projecting slightly beyond hinge line; adductor muscle field subquadrate, raised on shallow platform and with smaller posterior elements, divided by median ridge and extending anteriorly for 52% of length of the brachial valve.

MATERIAL AND LOCALITIES. Lectotype (Figs 316–7) BB 24077 (selected Cocks 1978 : 66), length 6.8 mm, width 8.6 mm, from loc. 50; also (colln O35) Fig. 320, BB 72458, length 4.1 mm, width 4.8 mm; Fig. 321, BB 72457, length 9.9 mm, width 12.8 mm; Fig. 323, BB 72456, est. length 10.5 mm, width 15.0 mm; Fig. 324, BB 72455, length 7.4 mm, width 8.9 mm; Fig. 328, BB 72459, length 8.4 mm, width 10.4 mm; Fig. 329, BB 72463, length 5.2 mm, width 6.8 mm; Fig. 330, BB 72462, length 11.4 mm, width 13.8 mm; Fig. 335, BB 72460, length 9.1 mm, width 12.6 mm. Lectotype of *inconstans* (Figs 318–9) BB 10259, length 11.1 mm, width 12.3 mm, from loc. 49, also (colln O98) Fig. 322, BB 72448; Fig. 325, BB 72450; Fig. 326, BB 72447; Fig. 327, BB 72449; Figs 331–4, BB 72451–4, also in the Onny Shale Formation.

DISCUSSION. See p. 261.

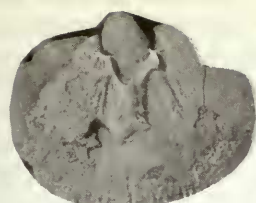
Onniella depressa Bancroft

Figs 294–315

- 1945 *Onniella depressa* Bancroft : 218–221; pl. 30, figs 10–13.
 1945 *Onniella sinuata* Bancroft : 222; pl. 30, figs 14–15.

DESCRIPTION (emended). Subcircular to subquadrate unequally biconvex *Onniella*, with evenly

Figs 306–331 *Onniella depressa* Bancroft, internal and external moulds of brachial valves: 306 = BB 72442, $\times 2.5$, 307 = BB 72438, $\times 2.5$, 308 = BB 72465, $\times 3$, 309 = BB 72440, $\times 3$, 310 = BB 72446, $\times 3$, 311 = BB 72464, $\times 2.5$, 312 = BB 72436, $\times 2.5$, 313 = BB 72439, $\times 2.5$, 314 = BB 72445, $\times 2.5$, 315 = BB 72437, $\times 2.5$. *Onniella broeggeri* Bancroft, conjoined valves: 316–7 = pedicle and brachial views respectively of lectotype BB 24077, $\times 2.5$, 318–9 = pedicle and brachial views respectively of BB 10259 (lectotype of synonymized *O. inconstans*), $\times 1.5$; internal moulds of brachial valves: 320 = BB 72458, $\times 5$, 321 = BB 72457, $\times 2.5$, 322 = BB 72448, $\times 2.5$, 323 = BB 72456, $\times 2.5$, 324 = BB 72455, $\times 3$, 325 = BB 72450, $\times 2.5$, 326 = BB 72447, $\times 2.5$, 327 = BB 72449, $\times 2.5$; internal moulds of pedicle valves: 328 = BB 72459, $\times 2.5$, 329 = BB 72463, $\times 4$, 330 = BB 72462, $\times 2.5$, 331 = BB 72454, $\times 2.5$.



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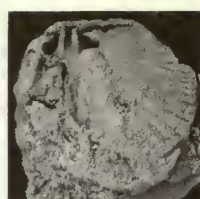
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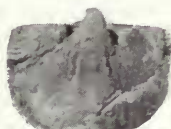
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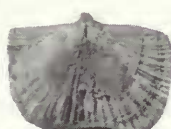
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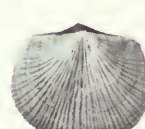
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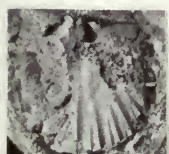
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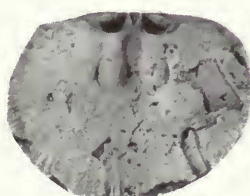
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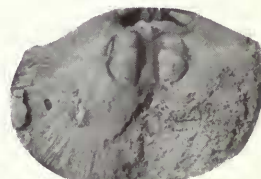
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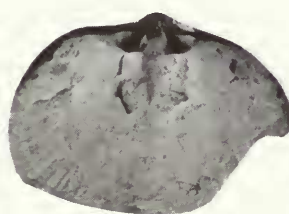
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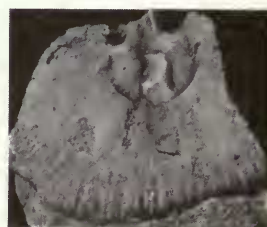
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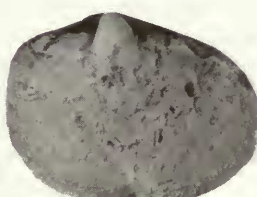
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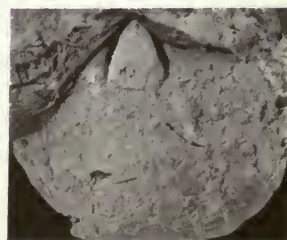
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convex, deeply sulcate brachial valve 79% as long as wide, and a pedicle valve 83% as long as wide and 34% as deep as long; dorsal interarea short, slightly curved, anacline, notothyrium open; ventral interarea short, curved, apscaline, delthyrium open; radial ornamentation commonly 6 costellae per mm, 2 mm anterior of dorsal umbo, branching freely developed.

Ventral interior with massive teeth supported by subparallel dental lamellae which extend anteriorly for 23% of the length of the valve and have weak or moderately strong crural fossettes on their inner faces; adult ventral muscle field angular cordate to subpentagonal and extending anteriorly for 35% the length of the pedicle valve, maximum width 32% of the valve length; elongate oval diductor lobes do not surround median lanceolate adductor scar.

Dorsal interior with massive cardinalia 18% as long as the brachial valve and 34% as wide as the valve length; brachiophores slightly divergent with weakly divergent bases, commonly expanded by secondary shell deposition to form thick triangular pads ankylosed to median ridge by ancillary struts; inner faces of brachiophore with pits; cardinal process with thick shaft posteriorly bilobed and crenulated, filling notothyrium and projecting slightly beyond hinge line; adductor scar subquadrate with smaller posterior elements, divided by median ridge and extending anteriorly for 48% the length of the brachial valve.

MATERIAL AND LOCALITIES. Lectotype (Figs 296–7) BB 10251 (selected Cocks 1978 : 66), length 12.7 mm, width 14.8 mm, from loc. 37, also (colln O24) Fig. 298, BB 72435, length 5.2 mm, width 6.8 mm; Fig. 300, BB 72434, length 7.8 mm, width 10.0 mm; Fig. 302, BB 72433, length 13.5 mm, width 16.8 mm; Fig. 307, BB 72438, length 7.1 mm, width 9.4 mm; Fig. 312, BB 72436, length 10.6 mm, est. width 11.0 mm; Fig. 315, BB 72437. Lectotype for *sinuata* Figs 294–5, BB 10254, length 10.7 mm, width 11.8 mm, from loc. 40. From loc. 41, colln O104, Fig. 310, BB 72446, Fig. 314, BB 72445; also colln O105, Fig. 301, BB 72444, Figs 304–6, BB 72441–3, Fig. 309, BB 72440, Fig. 313, BB 72439. From loc. 44, colln OA29, Fig. 299, BB 72466, Fig. 308, BB 72465, Fig. 311, BB 72464, also colln OA30, Fig. 303, BB 73679, length 11.6 mm, width 14.3 mm. Also recorded from locs 36, 38 and 39, all in the Acton Scott Formation.

DISCUSSION. See p. 261.

Onniella reuschi Bancroft

Figs 268–293

1928a *Onniella reuschi* Bancroft : 57–58; pl. 2, figs 10–13.

1945 *Onniella reuschi* Bancroft; Bancroft : 215–217; pl. 29, figs 1–6; pl. 30, figs 1–3.

1945 *Onniella grandis* Bancroft : 217; pl. 29, figs 7, 8, 14; pl. 30, figs 4–6.

1945 *Onniella aspasia* Bancroft : 217–218; pl. 29, figs 10–12; pl. 30, figs 7–9.

1958 *Onniella reuschi* Bancroft; Dean : pl. 25, figs 5–6.

1963 *Onniella grandis* Bancroft; Williams & Wright : pl. 1, figs 1, 5, 8; pl. 2, fig. 5.

DESCRIPTION (emended). Large, subcircular unequally biconvex *Onniella*, with evenly convex weakly sulcate brachial valve 74% as long as wide and about one-ninth as deep as long, and a pedicle valve 80% as long as wide and 22% as deep as long; dorsal interarea short, straight, anacline, notothyrium open; ventral interarea short, curved, apscaline, delthyrium open; radial ornamentation commonly 7 costellae per mm, 2 mm anterior of dorsal umbo, internal branching predominantly developed in sectors I to IV.

Ventral interior with strong, massive teeth supported by divergent dental plates which extend anteriorly for 19% of the length of the valve and have very weak crural fossettes on their inner faces; adult ventral muscle field rounded cordate and extending anteriorly for 34% the length of the pedicle valve, maximum width 31% of the valve length; oval diductor lobes do not surround median lanceolate adductor scar.

Dorsal interior with massive subparallel brachiophores which extend anteriorly for 17% of the valve length and splay laterally for 31% of the valve length; brachiophore secondarily thickened and with divergent bases; ancillary struts strong; cardinal process consisting of thick shaft posteriorly continuous with median ridge and with massive, ovoid, posteriorly crenulated, bilobed myophore, completely filling notothyrium and projecting slightly posterior of hinge line; thick

median ridge divides poorly-impressed adductor scars which extend anteriorly for 47% of the length of the valve.

MATERIAL AND LOCALITIES. Lectotype BB 10236 (selected Cocks 1978 : 66), length 8.2 mm, width 10.9 mm, from loc. 25, as is Fig. 283, BB 72408, length 12.7 mm, width 17.6 mm (colln WFT7). Also loc. 28, collns M10 and M11, including Figs 268–271, BB 72412–5, Figs 282, 284, 293, BB 72409–11. Loc. 46, Fig. 281, BB 10239 (lectotype of *grandis*, length 13.8 mm, width 17.0 mm) also (colln AS5) Figs 272, 273, 280, 285–7, BB 72417–22. Loc. 35, Fig. 274, BB 10248 (lectotype of *aspasia*, length 13.8 mm, width 17.0 mm) and colln DH1, Figs 275–7, 288–290, BB 72423–8. Loc. 47, colln CF4, Figs 278–9, 291–2, BB 72429–32. Also recorded from locs 22, 33–5, 43–5.

DISCUSSION. *Onniella* is abundant in the uppermost Crosspipes Member, Acton Scott Formation and Onny Shale Formation. Bancroft (1928a : 56–57) erected two species from the Upper Caradoc, *O. reuschi* and *O. broeggeri*, the latter of which he designated 'genotype'. He subsequently (1945 : 211–222) erected a series of seven species (five of them new) which, arranged in stratigraphical order, are *O. reuschi*, *O. grandis*, *O. aspasia*, *O. depressa*, *O. sinuata*, *O. inconstans* and *O. broeggeri*. He considered there to be two phylogenetic groups (1945 : 215), firstly the group of *O. grandis* forms, which encompassed *O. reuschi*, *O. grandis*, *O. aspasia*, *O. depressa* and *O. inconstans*. Bancroft claimed this group exhibited multiple progressive trends which were continuous and unidirectional. *O. aspasia* and *O. inconstans* were considered to be slightly divergent from the main lines of descent. The second group was that of *O. broeggeri*, which also includes *O. sinuata*.

Distinction between the seven species and the two species groups he drew in terms of shell size (an unreliable feature owing to transport and other environmental controls), impression of muscle scars, ribbing densities and relative branching of internal and external costellae. As pointed out by Williams & Wright (1963) and Williams (1963), in Bancroft's study of *Howellites* he did not subject his data to tests of significance, so that chosen characters, particularly rib patterns, used for specific diagnosis may not have been as sufficiently different as he believed and thus so reliable taxonomically. Bancroft also erected some species of *Onniella* on only a limited amount of material and often with little knowledge of the internal structures and variation. For example, he erected *O. sinuata* on a small number of conjoined valves and only one dorsal interior; apparently he had no ventral interiors.

For the present study large collections of topotypic material were obtained, as well as accessory populations (e.g. colln M11 corresponds to the cotype material used by Bancroft in describing *O. reuschi*, colln CF4 is an Actonian population of *O. reuschi* and colln O33 is stratigraphically the highest population of any *Onniella* in the Caradoc area and is assigned to *O. broeggeri*). The statistical data given in Tables 74–82 are based on these collections.

As regards bivariate statistics, species were arranged in stratigraphical order and each population tested against those adjacent. The topotype population (WFT7), cotype population (M11) and colln CF4 do not differ from each other in bivariate or other characters and are treated as the species *O. reuschi*. Also population O33 does not differ from topotype *O. broeggeri*.

O. reuschi (WFT7) differs from *O. grandis* solely in having a slower increase in width of the dorsal cardinalia ($P < 0.05$), yet *O. grandis* and *O. aspasia*, *O. reuschi* (WFT7) and *O. aspasia* do not differ as regards bivariate characteristics. *O. reuschi* differs from *O. depressa* in having a relatively narrower brachial valve ($P < 0.05$) and a slower increase in length of the dorsal cardinalia ($P < 0.05$). However, *O. reuschi* and *O. depressa* do not differ from *O. inconstans*, which itself does not differ from *O. reuschi* (WFT7) or *O. broeggeri*. Further, *O. broeggeri* does not differ from the topotype or cotype populations of *O. reuschi*, or from the Actonian population CF4.

In summary, bivariate statistics show that the seven 'species' of *Onniella* are very similar morphologically and do not segregate into neat species patterns. Thus it is misleading for Bancroft (1945) to distinguish

1. *O. reuschi* from *O. grandis* in terms of the greater size and larger muscle field of the latter
2. *O. aspasia* from *O. grandis* in terms of the delicate nature of the crural plates and smaller dorsal muscle area of the former

3. *O. depressa* from the remaining species by its relatively long shell and rounded contour
4. *O. broeggeri* by its small size, and
5. *O. inconstans* by the characteristic form of the valves.

Although the length/width relationship of the adult ventral muscle field (in valves above 4 mm in length) does not change relative proportions from species to species, the actual configuration of the scar does show changes of shape. There are two basic ventral muscle field configurations, here referred to as 'U'- and 'V'-shaped (Fig. 352). Table 83 lists the distribution of pedicle valves with the various muscle field shapes, from the topotype populations. Chi-squared (χ^2) tests show there to be three morphological groups in which the component species do not differ significantly:

1. *O. reuschi*, *O. grandis* and *O. aspasia*
2. *O. depressa* and *O. sinuata*
3. *O. inconstans* and *O. broeggeri*

All three species of Group 1 have predominantly U-shaped muscle fields and differ significantly ($P < 0.05$) from both species of Group 2, which have approximately equal U- and V-shaped muscle fields. They also differ from both species of Group 3 ($P < 0.01$), which have a predominantly V-shaped muscle field. Both species of Group 2 differ from both Group 3 species ($P < 0.05$).

Strength of the crural fossettes varies amongst the seven 'species'. On specimens above 4 mm in length these have been categorized as absent, weak or strong. The distributions for the topotype populations are shown in Table 84. Chi-squared (χ^2) tests again define the same three groups, with the component species not significantly different. All species of Group 1 differ from Group 2 and 3 species ($P < 0.01$ in each case) in having weak or absent crural fossettes. Group 2 species, with strong or weak crural fossettes, differ significantly from Group 3 species ($P < 0.01$), which have predominantly strong crural fossettes.

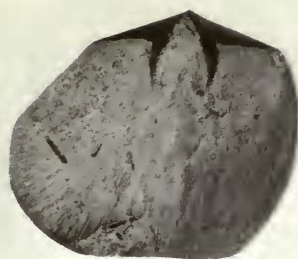
As noted by Bancroft (1945), the impression of the dorsal muscle field of *Onniella* varies. Table 85 lists the distribution of brachial valves with strongly or weakly impressed dorsal adductor scar. The following two groups are evident, in which the component species do not differ significantly:

1. *O. reuschi*, *O. grandis*, *O. aspasia*, *O. depressa* and *O. sinuata*
2. *O. inconstans* and *O. broeggeri*

Group 1 species, with a weakly-impressed dorsal adductor scar, differ significantly from Group 2 species ($P < 0.01$), which have a strongly-impressed adductor scar.

Bancroft mainly defined *Onniella* species on their ribbing patterns. Consequently, costellae densities as well as costellae insertions have been analysed (see Tables 86, 87). For costellae densities data were grouped into 5/6 and 7/8 costellae and tested for significance. *O. reuschi*, *O. aspasia* and *O. grandis* do not differ significantly. The former two have slightly finer ribbing and differ significantly ($P < 0.05$) from the slightly coarser-ribbed *O. depressa* and *O. sinuata*, which themselves are similar and also do not differ significantly from *O. inconstans* and *O. broeggeri*. *O. grandis* does not differ significantly from any species. In conclusion, although there is a general trend for finer-ribbed species to occur in the top of the Cheney Longville Formation (i.e. *O. reuschi*) and lower Acton Scott Formation (i.e. *O. grandis* and *O. aspasia*), and for coarser-ribbed species to occur in the upper Acton Scott Formation (i.e. *O. depressa* and *O. sinuata*) and Onny Shale Formation (i.e. *O. inconstans* and *O. broeggeri*), much of the variation is not significant.

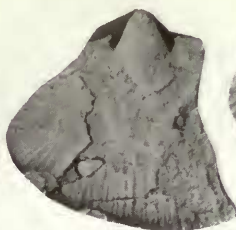
Figs 332–351 *Onniella broeggeri* Bancroft, internal moulds of pedicle valves: 332 = BB 72451, $\times 2.5$, 333 = BB 72452, $\times 2.5$, 334 = BB 72453, $\times 2.5$, 335 = BB 72460, $\times 2.5$. *Horderleyella* cf. *plicata* Bancroft, internal moulds of pedicle valves: 336 = BB 72492, $\times 2.5$, 337 = BB 72493, $\times 1.2$; internal and external moulds of brachial valves: 338 = BB 72494, $\times 1.4$, 339 = BB 72495a, $\times 1.2$, 340 = BB 72495b, $\times 0.9$. *Reuschella bilobata* (J. de C. Sowerby), internal moulds of pedicle valves: 341 = BB 9269 (lectotype of synonymized *R. semiglobata*), $\times 1.5$, 342 = BB 72508, $\times 1$, 343 = BB 72509, $\times 0.9$, 344 = BB 72507, $\times 0.9$; internal and external moulds of brachial valves: 345 = BB 72505, $\times 1.1$, 346 = BB 72506, $\times 1$, 347 = BB 72504b, $\times 1.3$, 348 = BB 72504a, $\times 2$, 349 = BB 72503, $\times 0.9$. Internal mould of pedicle valve of *Triplexia* sp.: 350 = BB 72370, $\times 3$. Internal mould of pedicle valve of *Bicuspina* sp.: 351 = BB 72371, $\times 3$.



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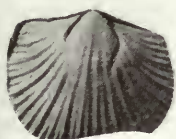
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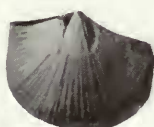
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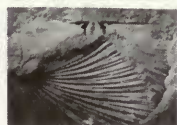
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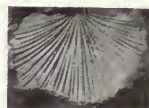
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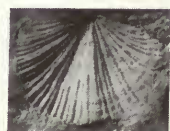
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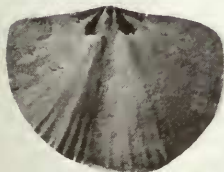
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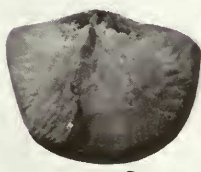
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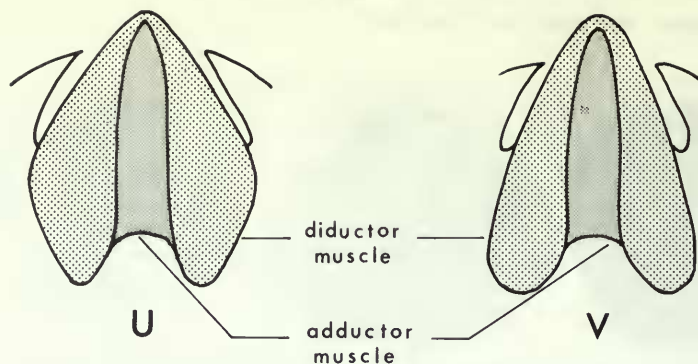


Fig. 352 Diagrammatic representation of the U- and V-shaped pedicle muscle fields of *Onniella*.

The earlier insertion of eight costellae relative to eight others has been analysed (Table 87); the data for *O. broeggeri* are from Williams (1963 : 408). 1b̄1ā are constantly fairly evenly associated throughout all seven 'species'. With regard to the earlier insertion of 2b̄2ā, both *O. depressa* and *O. sinuata* are similar and differ significantly ($P < 0.05$) from the remaining species in the earlier insertion of 2ā. *O. inconstans* and *O. broeggeri* have similar insertion rates for 2ā1̄2b̄ and differ significantly ($P < 0.05$) from the remaining species in the earlier insertion of 2b̄. Rib patterns 3ā1̄ā)3ā and 3ā1̄ā)2ā are constant throughout all seven species, with the earlier insertion of 3ā and 2ā respectively. 3ā is also regularly inserted earlier than 3c̄ in all seven species. Regarding 3ā1̄)2b̄1̄, *O. depressa* and *O. sinuata* have similar insertion rates, but in having the earlier insertion of 3ā1̄ differ significantly from the remaining species ($P < 0.05-0.01$). With the insertion of 4b̄)4b̄ *O. inconstans* and *O. broeggeri* are similar, yet significantly differ ($P < 0.001$) from the remaining species in the earlier insertion of 4b̄.

In summary, *O. reuschi*, *O. grandis* and *O. aspasia* are conspecific, as are *O. depressa*/*O. sinuata* and *O. inconstans*/*O. broeggeri*. Consequently, three species are recognized, *O. reuschi*, *O. depressa* and *O. broeggeri*. They differ in the configuration of the ventral muscle field and the strength of the crural fossettes. Further, *O. broeggeri* can be distinguished by its more heavily impressed quadripartite dorsal adductor muscle field, the significantly earlier insertion of both 2b̄ relative to 2ā1̄ and 4b̄ relative to 4b̄. *O. depressa* can be further distinguished by the significantly earlier insertion of 2ā relative to 2b̄ and 3ā1̄ relative to 2b̄1̄. *O. reuschi* tends to have the finest ribbing although the distribution within a population is not significantly different from *O. depressa* and *O. broeggeri*.

Family **HARKNESSELLIDAE** Bancroft, 1928

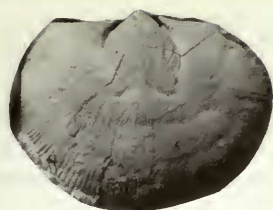
Genus **HORDERLEYELLA** Bancroft, 1928

Horderleyella cf. *plicata* Bancroft

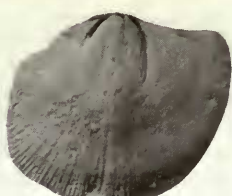
Figs 336-340

1928b *Horderleyella plicata* Bancroft : 186-187; pl. 1, figs 15-18.

Figs 353-378 *Heterorthina notata* (Barrande), internal moulds of pedicle valves: 353 = BB 72342, $\times 1.6$, 354 = BB 72341, $\times 1.6$, 355 = BB 72346, $\times 1.6$, 356 = BB 73683, $\times 1.8$, 357 = BB 73684, $\times 1.8$, 358 = BB 72345, $\times 2.1$, 359 = BB 72343, $\times 1.6$, 360 = BB 72344, $\times 1.8$; internal and external moulds of brachial valves: 361 = BB 72340, $\times 1.7$, 362 = BB 72347, $\times 2.2$, 363 = BB 72337, $\times 1.5$, 364 = BB 72338, $\times 1.2$, 365 = BB 72339, $\times 1.1$, 366 = BB 73682, $\times 1.3$. *Heterorthina praeculta* Bancroft, internal moulds of pedicle valves: 367 = BB 72284, $\times 1.3$, 368 = BB 72285, $\times 1.5$, 369 = BB 72286, $\times 1$, 370 = BB 72287, $\times 1.2$; internal and external moulds of brachial valves: 371 = BB 72288a, $\times 1.6$, 372 = BB 72288b, $\times 1.2$, 373 = 72291a, $\times 1.2$, 374 = BB 72291b, $\times 1.2$, 375 = BB 72289b, $\times 1.3$, 376 = BB 72289a, $\times 1.8$, 377 = BB 72290b, $\times 1.1$, 378 = BB 72290a, $\times 1.3$.



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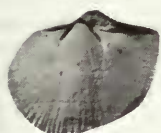
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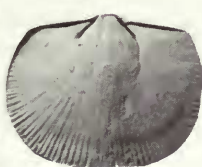
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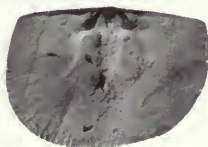
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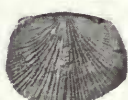
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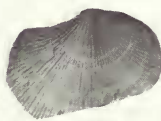
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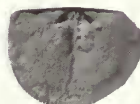
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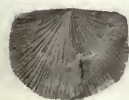
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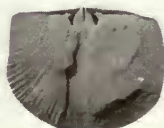
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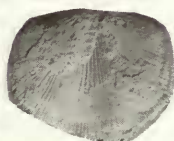
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1945 *Horderleyella plicata* Bancroft : 236–237; pl. 31, figs 4–7; pl. 32, figs 1–4.

1974 *Horderleyella* cf. *plicata* Bancroft; Williams : 102–103; pl. 16, figs 17, 19, 20; pl. 17, fig. 1.

DESCRIPTION. Ventribiconvex *Horderleyella* with right-angled cardinal margins, brachial valve approximately seven-tenths as long as wide and one-fifth as deep as long, pedicle valve three-quarters as long as wide and up to one-third as deep as long, and varying from weakly convex carinate forms to strongly convex non-carinate forms, ventral interarea long, slightly curved apscaline, delthyrium open, dorsal interarea short flat anacline, notothyrium open; radial ornamentation fascicostellate and ornamented by 4 or 5 fascicostellae per mm, 2 mm antero-medially of the dorsal umbo.

Ventral interior with small teeth and weak crural fossettes, supported by short divergent dental lamellae which extend anteriorly for one-seventh the valve length and extend forward as fairly strong ridges peripheral to the muscle field and curving back to the mid-line; ventral muscle scar bilobed, one-third as long as the valve and one-fifth as wide as the valve is long, and consisting of a narrow, elongately oval median adductor impression not enclosed by triangular diductor tracks.

Dorsal interior with cardinal process consisting of short, slender shaft expanding anteriorly for one-sixth the valve length and splaying laterally for one-quarter of the length of the valve, fulcral plates defining sockets; muscle field obscure.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72492	7.3 (est.)	8.9 (est.)
Internal mould of pedicle valve, BB 72493	14.2	16.8
Internal mould of brachial valve, BB 72494	10.5 (est.)	14.2
Internal and external mould of brachial valve, BB 72495a, b	13.0	17.6

HORIZON AND LOCALITIES. BB 72492 from colln H, loc. 31. BB 72493, BB 72494 and BB 72495a, b from colln M11, loc. 28.

DISCUSSION. A small number of moulds recovered from the Crosspipes Member (Marshbrookian) appear to be conspecific with *H. plicata* Bancroft from the Costonian and Harnagian of the type Caradoc. *H. plicata* may possibly be slightly coarser ribbed, but that aside this stock appears to have undergone little morphological change through the period Costonian–Marshbrookian.

Genus *REUSCHELLA* Bancroft, 1928

TYPE SPECIES. *Reuschella semiglobata* Bancroft by original designation of Bancroft (1928b : 180), treated here as a junior subjective synonym of *Orthis bilobata* J. de C. Sowerby.

Reuschella bilobata (J. de C. Sowerby) Figs 341–349

1839 *Orthis bilobata* J. de C. Sowerby in Murchison : 640; pl. 19, fig. 7.

1869 *Orthis vespertilio* J. de C. Sowerby; Davidson : 236 *pars*; pl. 30, figs 11, 17, 18, *non* figs 12–16.

1928b *Reuschella semiglobata* Bancroft : 188–190; pl. 2, figs 9–12.

1945 *Reuschella bilobata* (J. de C. Sowerby) Bancroft : 239.

DESCRIPTION. Strongly dorsibiconvex subquadrate *Reuschella* with rounded cardinal margins, brachial valve approximately three-quarters as long as wide and one-third as deep as long with a very shallow sinus, pedicle valve slightly concave in cross-section parallel to hinge and approximately three-quarters as long as wide and with a mean depth relative to length of one-eighth at the sharp median carina, lateral folds undulate; ventral interarea long, curved apscaline, delthyrium open, dorsal interarea short, flat anacline and with open notothyrium; radial ornamentation medium to coarsely fascicostellate.

Ventral interior with massive teeth and supported by divergent to subparallel dental plates which extend anteriorly for one-quarter the valve length and extend forward as strong ridges peripheral to muscle field; ventral muscle scar bilobed, two-fifths as long as valve and one-third

as wide as valve length, and consisting of a narrow lanceolate median adductor impression not enclosed by elongate triangular diductor tracks.

Dorsal interior with cardinal process consisting of massive rounded shaft and crenulated, ridged bulbous myophore completely filling notothyrium, notothyrial platform massive and indented anteriorly by moderately deep pits of adductor muscle scar, brachioophores divergent, extending anteriorly for one-seventh of the valve length and splaying laterally for one-third of the valve length, sockets deep and crenulated, muscle scar obscure.

MATERIAL AND LOCALITIES. Lectotype (selected Cocks 1978 : 76) GSM Geol. Soc. Colln GSd 5527, from Acton Scott Formation, 'Acton Scott' (exact locality unknown). Lectotype of *semiglobata* (Fig. 341) BB 9269, length 25.7 mm, width 31.0 mm, from loc. 42. Loc. 24, colln WFT1, e.g. Fig. 349, BB 72503, length 24.4 mm, width 29.5 mm; also colln WFT2, e.g. Figs 347–8, BB 72504, length 11.4 mm, width 15.0 mm. Loc. 1, colln CL7, e.g. Fig. 342, BB 72508, length 25.1 mm, width 33.3 mm. Loc. 44, colln OA25, e.g. Fig. 345, BB 72505, length 23.8 mm, width 36.2 mm. BB 72509 (Fig. 343), BB 72507 (Fig. 344) and BB 72506 (Fig. 346) are with no precise locality labels, but are probably from loc. 47. Known from locs 1–48.

DISCUSSION. *Reuschella* occurs throughout the Alternata Limestone to Acton Scott Formation but never in any abundance. J. de C. Sowerby in Murchison (1839) described *Orthis bilobata* from some part of this sequence. Bancroft (1928b), when he erected *Reuschella*, commented on the fact that *O. bilobata* belonged to *Reuschella*, but because it was not precisely located and known only by the interior of the brachial valve he ignored it. Instead, he erected *R. semiglobata*, saying it differed from *R. bilobata* in having small wings, a more conspicuous sinus in the brachial valve, absence of well-defined dorsal muscle scars and in having a greater longitudinal extension of the crural plates.

New collections, and examination of Bancroft's type material, show *R. semiglobata* to be a variable stock within which is encompassed the single figured specimen of *R. bilobata*. Thus *R. semiglobata* is treated as a synonym of *R. bilobata*. Further, all post-Lower Longvillian *Reuschella* specimens are assigned to *R. bilobata*.

Bancroft (1928b) described *R. horderleyensis* from pre-Upper Longvillian strata, in the type Caradoc. He did, however, note that in terms of shell shape some *R. horderleyensis* specimens are comparable to *R. bilobata*. However, until more is known of the variability of *R. bilobata* the two species are best kept separate.

Family **HETERORTHIDAE** Schuchert & Cooper, 1931

Genus **HETERORTHIS** Hall & Clarke, 1892

Heterorthis alternata (J. de C. Sowerby)

- 1839 *Orthis alternata* J. de C. Sowerby in Murchison : 638; pl. 19, fig. 6.
 1871 *Orthis alternata* J. de C. Sowerby; Davidson : 264 *pars*; pl. 31, figs 7–8, *non* figs 1–6.
 1963 *Heterorthis alternata* (J. de C. Sowerby) Williams : 418; pl. 9, figs 1–6, 8, 9.

Williams (1963) has redescribed and figured this species, and his work will not be duplicated here. The species occurs at locs 1–8 inclusive and 44. Further, Dean (1958) reported a thin shell bed of *H. alternata* in the lowest Acton Scott Formation of the Onny Valley, but this is not now exposed, and Harper (1978) another thin shell bed in the Onny Shale Formation.

Genus **HETERORTHINA** Hall & Clarke, 1892

- 1928a *Heterorthina* Bancroft : 59.
 1960 *Elsaella* Alichova : 192.
 1975 *Elsaella* Alichova; Hints : 78.

DIAGNOSIS. Transverse, very gently and unequally biconvex heterorthids with more deeply convex pedicle valve and shallow, persistently sulcate brachial valve; ventral interarea short,

curved, apscaline with open delthyrium; dorsal interarea short, anacline; notothyrium completely filled by cardinal process; shell punctate; radial ornamentation multicostellate, of fine to very fine costellae with both external and internal branches freely developed in all sectors; costellae curving in posterior regions of shell to intersect hinge line.

Ventral interior with small teeth supported by short, blunt, divergent dental lamellae; pedicle callist well developed; muscle field large, elongately pentagonal, occasionally with semiflabellate diductor tracks, anteriorly not enclosing lanceolate adductor scar (very rarely anterior lobes of convergent diductor scars meet medially to surround adductor scars completely.)

Dorsal interior with strong cardinal process, anterior shaft with cleft, myophore expanded into large ovoid structure which early in ontogeny is bilobed but which with maturity develops up to four small septa dividing myophore into separate lobes; posterior end of myophore crenulated and extending well beyond hinge line; brachiophores greatly divergent, with divergent bases, fulcral plates absent; dorsal adductor scars elongate with approximately equal posterior and anterior elements.

TYPE SPECIES. *Heterorthina praeculta* Bancroft, by original designation of Bancroft (1928a : 59).

DISCUSSION. Bancroft (1928a : 59–60) erected this genus; whilst recognizing it was distinct from *Heterorthis alternata* (Sowerby) he noted that it shared many characteristics.

The assignment of *Heterorthina* to a suprageneric category was formerly unsettled. Williams & Wright (1963) placed it in the Dalmanellidae. Later Harper, Boucot & Walmsley (1969) questionably assigned the genus to the subfamily Heterorthinae Schuchert & Cooper, of the Rhipidomellidae Schuchert, 1913. It is now clear from the thorough work of Havlíček (1970) that *Heterorthina* should unquestionably be assigned to the Heterorthidae of Schuchert & Cooper, 1931. The diverging brachiophore bases and lobation of the cardinal process myophore into a bilobed, trilobed or quadrilobed structure suggest strong affinities with *Tafilaltia* Havlíček, 1970 and *Svobodaina* Havlíček, 1950. The configuration of the pedicle valve muscle field of *Heterorthina* also suggests such affinities. Such a line of derivation involved increasing complexity of the cardinal process myophore and lobation of the pedicle diductor muscle field. It is interesting to note that young specimens of the pedicle valves of *Svobodaina inclyta* (Barrande), figured by Havlíček (1970 : pl. 5), are remarkably similar, especially in diductor muscle scar configuration, to adult *Heterorthina*. Further, Havlíček (1970 : 23) notes that, rarely, the anterior lobes of the adductor scars of *Svobodaina* touch, to surround the adductor tracks completely, a feature also occasionally seen in *Heterorthina praeculta*.

Williams & Wright (1963) placed the genus *Elsaella* Alichova in synonymy with *Heterorthina*. Recently, Hints (1975) has brought *Elsaella* out of synonymy, believing the central position of the pedicle adductor scar, trilobed cardinal process and possibly the rhipidomellid type of ribbing warrant a separate genus. The trilobed cardinal process is common in *Heterorthina* and the central position of the pedicle adductor field is occasionally attained in *H. praeculta* through the medial expansion of the diductor tracks (see also Howe 1965 : text-fig. 6). The only apparent difference between the two genera is the coarser ribbing of *Elsaella*. These small differences do not warrant the retention of the separate genus *Elsaella*.

Heterorthina morgatensis Mélou

1975 *Heterorthina morgatensis* Mélou : 192–203; pl. 20, figs 1–9; pl. 21, figs 1–12; pl. 22, figs 1–5.

DESCRIPTION. Small, transverse, unequally biconvex *Heterorthina*, with weakly convex brachial valve 68% as long as wide; pedicle valve 71% as long as wide; delthyrium and notothyrium open, ventral interarea weakly curved apscaline; dorsal interarea short anacline; radial ornamentation of fine costellae 4 or 5 per mm, 5 mm anteromedially of dorsal umbo; costellae in posterior region curving to intersect hinge line.

Ventral muscle field strongly bilobed, flabellate, extending anteriorly for 61% of the length of the pedicle valve, but not surrounding the median adductor field; diductor scars 58% as wide as the pedicle valve is long.

Dorsal interior with broad, shallow median ridge, at posterior end of which arises the moderately thick cleft shaft of the cardinal process, which expands into bilobed myophore filling most of the notothyrium; brachiophores divergent, short, strong, with broad divergent bases extending forward for 21% of the length of the brachial valve and splaying laterally for 26% of the valve length; notothyrial platform poorly developed; sockets narrow and well-defined, without fulcral plates; adductor scars elongately oval, impressed quadripartite and extending anteriorly for 50% the length of the valve.

DISCUSSION. See p. 271.

Heterorthina notata (Barrande)

Figs 353–366

1879 *Orthis notata* Barrande : pl. 66, fig. II (*non* pl. 127, fig. VIII).

1932 *Heterorthis barrandei* Schuchert & Cooper : 137.

1950 *Heterorthina notata* (Barrande) Havlíček : 105–106; pl. VIII, figs 1, 2, 8, 10 and 13.

1975 *Heterorthina notata* (Barrande); Mélou : pl. 22, figs 8–9.

1977 *Heterorthina notata notata* (Barrande); Havlíček : 116; pl. 20, figs 18–24.

DESCRIPTION. Transverse, unequally biconvex *Heterorthina*, with evenly weakly convex, shallow sulcate brachial valve 76% as long as wide; pedicle valve 80% as long as wide and 18% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist large, ventral interarea weakly curved apscaline, dorsal interarea short anacline and with prominent growth lines; radial ornamentation of fine costellae commonly 4 per mm, 5 mm anteromedially of the dorsal umbo; costellae curve to intersect hinge line.

Ventral muscle field bilobed with diductor scars, showing well-developed growth increments, extending anteriorly for 42% of the length of the pedicle valve but not surrounding the elongately oval median adductor field; diductor scars 36% as wide as the valve is long; teeth very small, supported by short receding dental plates lacking crural fossettes and extending anteriorly for 15% of the length of the pedicle valve; shell ridge extensions of the dental plates bounding the lateral and anterior parts of the diductor scars.

Dorsal interior with broad median ridge, at posterior end of which arises very broad shaft of cardinal process; myophore extremely large, filling notothyrium, bilobed in individuals below 9 mm in length and trilobed or quadrilobed by septa in more mature specimens, crenulated posteriorly and extending well beyond hinge line; brachiophores divergent, short, very strong and with broad divergent bases, extending forward for 15% of the length of the brachial valve and splaying laterally for 26% of the valve length; notothyrial platform very well developed; well-defined narrow sockets lacking crural fossettes; adductor scars elongately suboval, impressed particularly posteriorly on either side of broad median ridge and extending anteriorly for 48% the length of the valve.

DIMENSIONS.

	length	width
Internal mould of brachial valve, BB 72337	14.0	17.0
Internal mould of brachial valve, BB 72338	15.7	20.8
Internal mould of brachial valve, BB 72339	18.0	23.0
Internal mould of brachial valve, BB 72340	16.2	20.0
Internal mould of brachial valve, BB 72347	9.1	12.1
External mould of brachial valve, BB 73682	11.4	13.0
Internal mould of pedicle valve, BB 72341	15.1	19.8
Internal mould of pedicle valve, BB 72342	15.6	21.4
Internal mould of pedicle valve, BB 72343	14.6	17.2
Internal mould of pedicle valve, BB 72344	17.5	20.8
Internal mould of pedicle valve, BB 72345	12.3	15.9
Internal mould of pedicle valve, BB 72346	13.4	18.0
Internal mould of pedicle valve, BB 73683	14.1	16.4
Internal mould of pedicle valve, BB 73684	8.7	11.8

HORIZON AND LOCALITIES. All figured material is from the type locality in a temporary trench along a railway line at Palmovka Hill, Praha – Libeň, Czechoslovakia; Beroun Series, Zahofany Formation.

DISCUSSION. See p. 271.

Heterorthis praeculta Bancroft

Figs 367–379

1928a *Heterorthis praeculta* Bancroft : 59–60; pl. 2, figs 14–21.

1963 *Heterorthis praeculta* Bancroft; Williams & Wright : 28; pl. 1, fig. 19.

1965 *Heterorthis praeculta* Bancroft; Wright in Williams *et al.*: H335.

1967 *Heterorthis macfarlanei* Neuman : A10–A12; pl. 2, figs 1–19.

1975 *Heterorthis praeculta* Bancroft; Mélou : 202; pl. 22, figs 6–7.

1975 *Heterorthis kerfornei* Mélou : 203–207; pl. 23, figs 1–14; pl. 24, figs 1–13.

DESCRIPTION. Transverse, unequally biconvex *Heterorthis* with an evenly weakly convex to flat, weakly sulcate brachial valve 76% as long as wide; pedicle valve 80% as long as wide and 24% as deep as the valve is long; delthyrium and notothyrium open, pedicle callist small, ventral interarea slightly curved apscaline, dorsal interarea short anacline; radial ornamentation of very fine costellae commonly 5 or 6 per mm, 5 mm anteromedially of the dorsal umbo; costellae in posterior region curve to intersect hinge line.

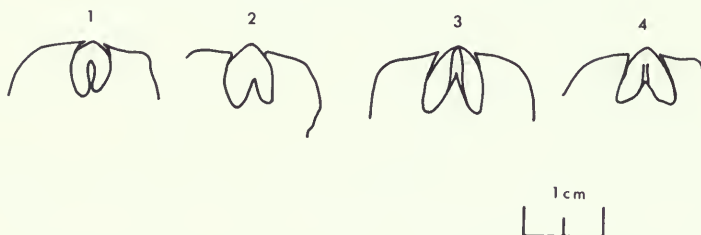


Fig. 379 Range of variation in pedicle musculature of *Heterorthis praeculta*.
Note variation from V to U shapes from 1 to 4.

Ventral muscle field bilobed with diductor scars extending anteriorly for 43% of the length of the pedicle valve but not surrounding the elongately oval median adductor scar (rarely adductor scar is surrounded), from which they are separated by shallow depressions (expressed as ridges in mould); diductor scars 39% as wide as the pedicle valve is long; teeth small, supported by short receding dental plates, extending anteriorly for 14% of the length of the pedicle valve and with strong crural fossettes; shallow ridges bound the diductor scars anteriorly.

Dorsal interior with broad median ridge, at posterior end of which arises broad, deeply cleft shaft of cardinal process; myophore large, bilobed or trilobed and crenulated posteriorly extending beyond hinge line; brachioophores short strong, divergent, with broad divergent bases, extending forward for 17% of the length of the brachial valve and splaying laterally for 31% of the length of the valve; sockets narrow, well-defined, without fulcral plates; adductor scars sub-oval, impressed on either side of median ridge and extending anteriorly for 47% the length of the valve.

MATERIAL AND LOCALITIES. Lectotype BB 9152 (selected Cocks 1978 : 74) from loc. 31, from which also comes all the material figured here, e.g. Fig. 367, BB 72284, length 17.0 mm, width 20.0 mm; Fig. 368, BB 72285, length 9.0 mm, width 10.0 mm; Fig. 369, BB 72286, length 17.0 mm, width 19.8 mm; Fig. 370, BB 72287, length 16.5 mm, width 21.0 mm; Figs 371–2, BB 72288, length 15.3 mm, width 18.6 mm; Figs 373–4, BB 72291, length 10.6 mm, width 13.6 mm; Figs 375–6, BB 72289, length 8.3 mm, width 12.2 mm; Figs 377–8, BB 72290, est. length 17.0 mm, width 20.5 mm. Also recorded from locs 11, 29 and 32.

Outside Britain the species is known from the Grier Limestone Member of the Lexington Limestone (Soudleyan–Longvillian) of North America, and the Schistes de Postolonnec (Caradoc) of Brittany, France.

DISCUSSION. A topotypic sample of *H. praeculta* has been statistically compared with *H. macfarlani* (data given by Neuman 1967 : A11 and Mélou 1975 : 201–202) from the Grier Limestone Member of the Lexington Limestone, U.S.A. (Soudleyan – Longvillian ?), *H. kerfornei* (data given by Mélou 1975 : 205–206) from the Schistes de Postolonnec (Caradoc), France, and *H. morgatensis* (data given by Mélou 1975 : 197–198), also from the Schistes de Postolonnec (Tables 88–96). The comparisons show that *H. macfarlani* and *H. kerfornei* do not differ significantly from *H. praeculta*.

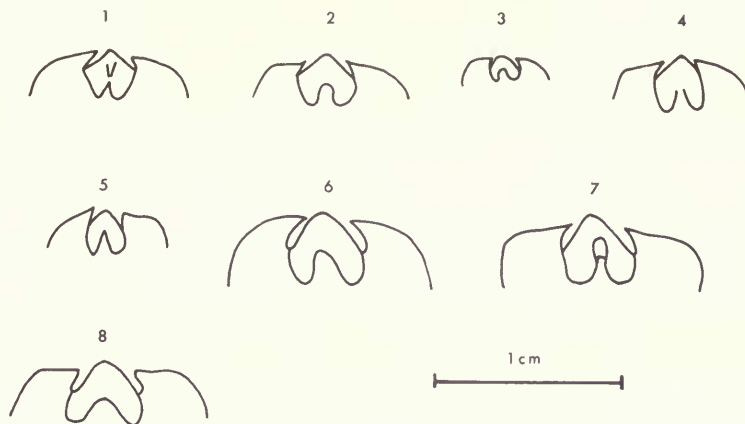


Fig. 380 Range of variation in pedicle musculature of *Heterorthina kerfornei*. Note variation from V to U shapes from 1 to 8.

Mélou (1975 : 206) claims that *H. kerfornei* differs significantly from *H. praeculta* in terms of size, form of the ventral muscle field and morphology of the cardinal process. Absolute size as a taxonomic character is unreliable and the relative dimensions of the ventral muscle fields do not differ significantly. Further, the overall diductor muscle field variation expressed by a population of *H. praeculta* (Fig. 379) is contained within the same variation limits as *H. kerfornei* (Fig. 380). From the figured specimens of *H. kerfornei* populations appear to contain a predominance of individuals which have massive cardinal process shafts filling the notothyrial cavity. In *H. praeculta* the cardinal process shaft is more variable, with individuals having either massive or non-massive ones, and thus *H. kerfornei* populations appear to be end members of the variation of topotype *H. praeculta*. There are therefore no consistent significant morphological differences between *H. praeculta*, *H. macfarlani* and *H. kerfornei*, consequently the relationships between the three species are most conveniently expressed by assuming that they in fact represent a single species, *H. praeculta*.

H. morgatensis differs from *H. praeculta* in the significantly ($P < 0.005$) faster increase in relative length of the dorsal cardinalia. The dimensions of the ventral muscle field do not differ, yet the diductor tracks of *H. morgatensis* are frequently lobate whereas those of *H. praeculta* are not. Further, the cardinal process of the French species is very strongly bilobate, with a deep groove separating each lobe. From the figured specimens (Mélou 1975 : pl. 21) *H. morgatensis* has 4 (LPB 2798) or 5 (LPB 2800) costellae per mm, 5 mm anteromedially of the dorsal umbo, and so appears more coarsely ribbed than *H. praeculta*.

A topotypic sample of *H. notata* from near Prague differs significantly from *H. praeculta* in the slower relative width of the dorsal cardinalia ($P < 0.001$), the coarser ribbing (see Table 97; $P < 0.01$) and in lacking crural fossettes (Table 98; $P < 0.01$). The pedicle valve diductor tracks show a wide range of variation (Fig. 381) from simple pentagonal scars to exaggerated bilobed tracks, approaching those of *Svobodaina*. *H. notata* differs significantly from *H. morgatensis* in having a slower relative increase in dorsal cardinalia width ($P < 0.05$), and in having shorter dorsal cardinalia ($P < 0.05$). The ribbing of the two species approximates, yet the structure of the cardinal process is different.

One of the earliest-described species referred to *Heterorthina*, *H. fairmontensis* (Foerste, 1909 : 322) of Maysville age (Onnian – Purgillian), appears very similar to *H. praeculta*. Neuman (1967) considered the species to be very similar to *H. macfarlani*. Until more is known about the variation expressed by *H. fairmontensis* the two species are kept separate.

The configuration of the pedicle valve muscle field (i.e. the complete surrounding of the adductor scar by the diductor tracks), the coarse ribbing and the apparent lack of external branches in the first four sectors of ribbing in the brachial valve indicate that the type species of *Elsaella* is probably a distinct species of *Heterorthina*.

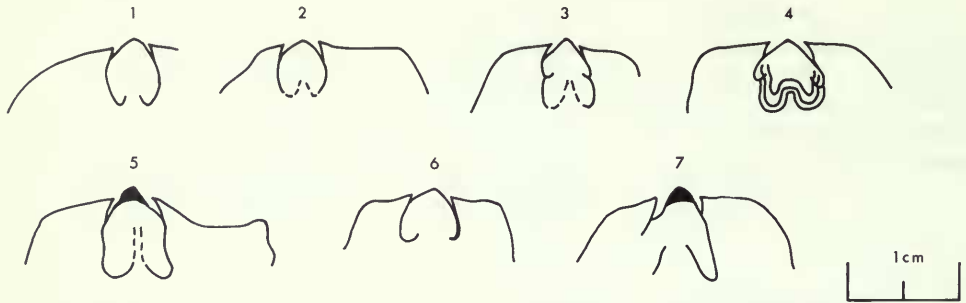


Fig. 381 Range of variation in pedicle musculature of *Heterorthina notata*.
Note variation from V to U shapes from 1 to 7.

Genus *MARIONITES* Cooper & Muir-Wood, 1951

DIAGNOSIS (emended). Subcircular heterorthiids with deeply and evenly convex brachial valve with narrow median sulcus, ventral valve weakly resupinate and carinate in transverse profile; radial ornamentation multicostellate with costellae directed posteriorly along hinge line, branching freely developed; ventral interarea short, straight orthocline to very weakly anacline, notothyrium open and filled by massive cardinal process.

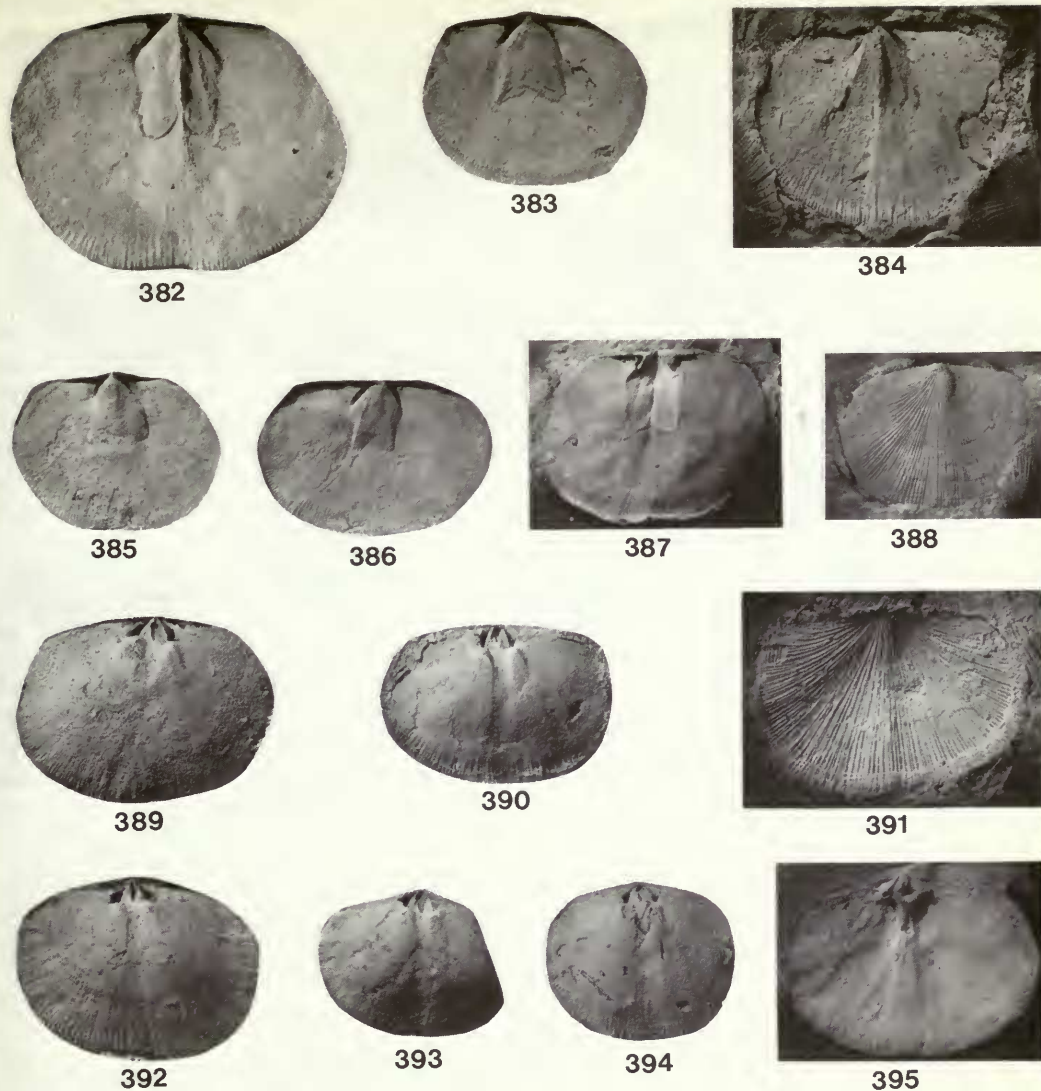
Ventral interior with massive teeth supported by thick, divergent, receding dental lamellae, pedicle callist well developed, muscle field flabellate surrounded by sinuous ridges, with submedian diductor lobes extending beyond, but not completely surrounding, median lanceolate adductor scar.

Dorsal interior with massive, incipiently bilobed cardinal process, brachiophores greatly divergent, brachiophore bases weakly to moderately divergent, notothyrial platform massive, ankylosed to brachiophore bases and extending anteriorly into broad median ridge, weak fulcral plates occasionally developed; dorsal adductor scars elongate with posterior elements deeply inserted into anterior region of notothyrial platform.

TYPE SPECIES. *Marionella typa* Bancroft, by original designation of Cooper & Muir-Wood (1951).

DISCUSSION. The taxonomic position of *Marionites* has been unstable. Bancroft (1928b) erected the genus *Marionella* and placed it in a new subfamily, the Harknessellinae, along with the genera *Harknessella* Reed, 1917, *Reuschella* Bancroft, 1928, *Smeathenella* Bancroft, 1928 and *Horderleyella* Bancroft, 1928. He thought that the genus was morphologically intermediate between *Harknessella* and the Rhipidomellidae. Subsequently, Schuchert & Cooper (1932) relegated *Marionella* to a subgenus of *Dinorthis*, a position with which Bancroft apparently agreed (Schuchert & Cooper 1932 : 96). They concluded that despite the lack of information regarding the punctate or impunctate nature of the shell, the internal features suggest dinorthiid affinities. The brachiopod name *Marionella*, being a junior homonym, was replaced by *Marionites* (Cooper & Muir-Wood 1951).

Williams *et al.* (1965) placed *Marionites* in the family Plaesiomyidae Schuchert, 1913, as a subgenus of *Multicostella* Schuchert & Cooper, 1931. The nature of the multicostellate ribbing of *Marionites* (i.e. posteriorly-directed costellae along the hinge line) clearly suggests this genus



Figs 382-395 *Marionites typus* (Bancroft), internal moulds of pedicle valves: 382 = lectotype BB 9126, $\times 2$, 383 = BB 72529, $\times 1.5$, 384 = BB 72532, $\times 2$, 385 = BB 72530, $\times 1.3$, 386 = BB 72531, $\times 1.3$; internal and external casts of pedicle valves: 387 = BB 9126, $\times 1.3$, 388 = BB 24626, $\times 1.3$; internal and external moulds of brachial valves: 389 = BB 72537, $\times 1.6$, 390 = BB 24627, $\times 1.7$, 391 = BB 72534b, $\times 1.9$, 392 = BB 72533, $\times 2.2$, 393 = BB 72536, $\times 1.2$, 394 = BB 24628, $\times 1.2$; internal cast of brachial valve: 395 = BB 9124, $\times 1.1$.

belongs in the Heterorthidae of Schuchert & Cooper 1931 (see Havlíček 1970 : 8-9; 1977 : 119). However, as the available material is preserved as internal and external moulds in sandstone, it is not known beyond doubt whether the shell was punctate, although it appears to be very finely so. Further, the nature of the flabellate ventral muscle scar, the massive elliptical cardinal process and brachioophore configuration are all suggestive of heterorthid affinities. None the less, in having a strongly convex brachial valve and resupinate and carinate pedicle valve *Marionites* resembles some members of the Harknessellidae. The similarity between *Marionites* and some genera of the Plaesiomyidae is a clear case of homoeomorphy. Havlíček's (1977) *Marionites*

resupinatus appears to fall within the variation of *M. typus*, but until this can be adequately demonstrated they are left as separate species.

***Marionites typus* (Bancroft)**

Figs 382–395

1928b *Marionella typa* Bancroft : 190–191; pl. 2, figs 13–16.

1932 *Marionella typa* Bancroft; Schuchert & Cooper : pl. 8, figs 16–18.

1951 *Marionites typa* (Bancroft) Cooper & Muir-Wood : 195.

1965 *Marionites typa* (Bancroft); Williams *et al.* : H321, fig. 202, 4a–d.

DESCRIPTION. Subcircular *Marionites* with evenly convex, weakly sulcate brachial valve 12% as long as wide and 28% as deep as long, and resupinate pedicle valve 75% as long as wide; radial ornamentation finely multicostellate, branching freely developed; dental lamellae strong, divergent and extending anteriorly for 15% the length of the pedicle valve, ventral muscle scar extending anteriorly for 49% the length of the valve and 38% as wide as the valve is long; massive cardinalia with divergent brachiophore bases extending anteriorly for 18% of the length of the brachial valve and 28% wide as the valve is long; dorsal adductor scar extending forward of umbo for 45% the length of the valve.

MATERIAL AND LOCALITIES. Lectotype (Figs 382, 387) BB 9126 (selected Cocks 1978 : 51), length 18.0 mm, width 23.5 mm, from loc. 1 (= Bancroft loc. N6). From the same locality came BB 72529 (Fig. 383), length 16.2 mm, width 21.1 mm, BB 72530 (Fig. 385), length 16.8 mm, width 22.3 mm; BB 72531 (Fig. 386), length 15.9 mm, width 24.3 mm; BB 72532 (Fig. 384), length 13.4 mm, width 16.7 mm; BB 72533 (Fig. 392), length 12.0 mm, width 15.3 mm; BB 72534 (Figs 390–1), length 13.5 mm, width 19.1 mm; BB 72535–6 (Figs 393–4); BB 9124 (Fig. 395); BB 24626 (Fig. 388). Also from loc. 7, colln S3, e.g. BB 72537 (Fig. 389), length 15.6 mm, width 22.1 mm. Also recorded from locs 5 and 6, all in the Alternata Limestone Formation.

Suborder **TRIPLESIIDINA** Moore, 1952
 Superfamily **TRIPLECIACEA** Schuchert, 1913
 Family **TRIPLECIIDAE** Schuchert, 1913

Genus **TRIPLESIA** Hall, 1859

Triplesia sp.

Fig. 350

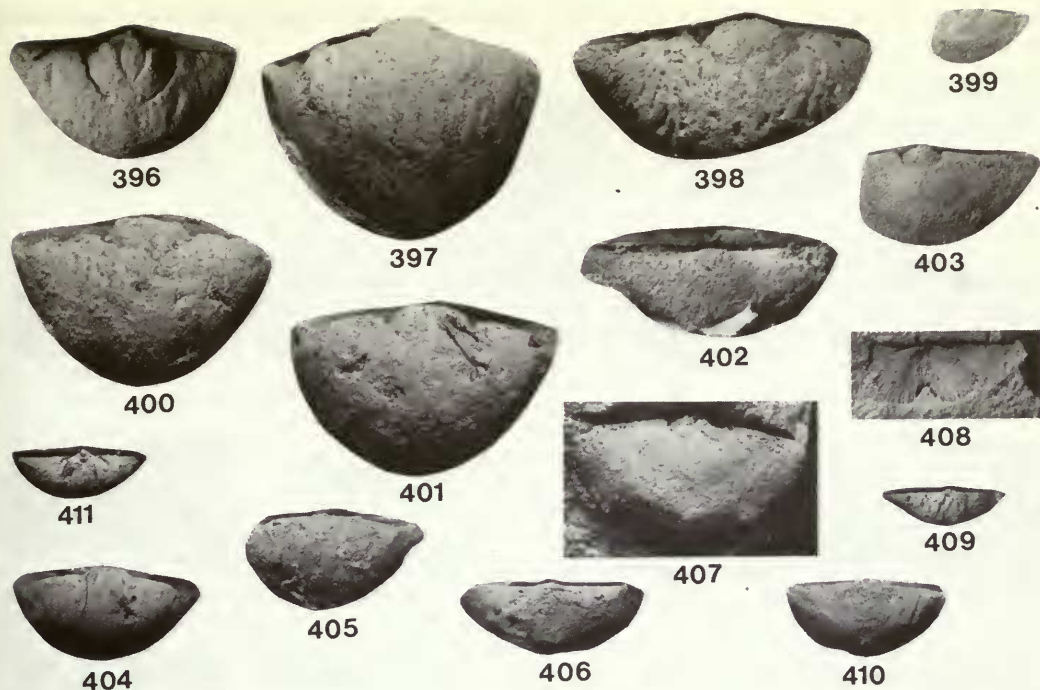
A distorted internal mould of a pedicle valve (BB 72370) from loc. 44, colln OA13 of the Acton Scott Formation is the sole representative of *Triplesia* in the Upper Caradoc rocks. The valve was approximately 4.5 mm long, 4.8 mm wide and 1.1 mm deep. Its outline was elongately subcircular, with rounded cardinal angles and a deep, slightly angular sulcus. Umbonal area crushed, but the dental lamellae appear short and widely splayed.

Genus **BICUSPINA** Havlíček, 1950

Bicuspina sp.

Fig. 351

A distorted internal mould of a pedicle valve (BB 72371) from loc. 43, colln CP4 is the sole representative of *Bicuspina* in the Upper Caradoc. The valve was approximately 6.5 mm long, 10.6 mm wide and 1.7 mm deep. Its outline was subquadrate, with a straight, wide hinge line and with a rounded sulcus. Dental plates thin and divergent; pedicle tube obscured.



Figs 396–411 *Leptestiina oepiki* (Whittington), internal moulds of pedicle valves: 396 = BB 72510, $\times 2.5$, 397 = BB 72510, $\times 3.0$, 398 = BB 72511, $\times 3$, 400 = BB 72509, $\times 3.2$, 401 = BB 72512, $\times 3.4$; external mould of brachial valve: 402 = BB 72513, $\times 3.2$. *Leptestiina* sp., internal moulds of pedicle valves: 399 = BB 72514, $\times 3$, 403 = BB 72515, $\times 3.7$, 407 = BB 72516, $\times 3$; internal mould of brachial valve: 408 = BB 72517, $\times 3.3$. *Eoplectodonta* cf. *rhombica* (M'Coy), internal moulds of pedicle valves: 404 = BB 72519, $\times 2$, 405 = BB 72518, $\times 1.8$, 409 = BB 72521, $\times 1.5$, 410 = BB 72520, $\times 2$, 411 = BB 72519, $\times 1.4$; external mould of brachial valve: 406 = BB 72522, $\times 1.8$.

Order STROPHOMENIDA Öpik, 1934
 Suborder STROPHOMENIDINA Öpik, 1934
 Superfamily PLECTAMBONITACEA Jones, 1928
 Family LEPTELLINIDAE Ulrich & Cooper, 1936
 Subfamily LEPTESTIININAE Havlíček, 1961

Genus *LEPTESTIINA* Havlíček, 1952

Leptestiina oepiki (Whittington)

Figs 396–398, 400–402

1938 *Sampo oepiki* Whittington : 255; pl. 10, figs 15–16; pl. 11, fig. 10.

1963 *Leptestiina oepiki* (Whittington) Williams : 428–430; pl. 10, figs 15, 16, 19–21.

aff.1977 *Leptestiina* aff. *oepiki* (Whittington); Mitchell : 76; pl. 15, figs 1–7.

DESCRIPTION. Elongate, semicircular *Leptestiina* with evenly concavo-convex longitudinal profile, with pedicle valve about 60% as long as wide and 40% as deep as long; ventral interarea apscaline, pseudodeltidium small and apical; ornamentation not known.

Ventral interior with very short blunt teeth, supported by short receding dental plates; ventral muscle field subpentagonal in outline, extending anteriorly for about 30% of the length of the pedicle valve and about 75% as long as wide, adductor field lanceolate, deeply impressed posteriorly and separated from adductor scars by ridges, diductor scars almost meeting anteriorly

to surround adductors, whole muscle field surrounded by shell ridges which fuse posteriorly with dental lamellae.

Brachial interior not known.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72509	6.5	10.9
Internal mould of pedicle valve, BB 72510	8.4	12.6
Internal mould of pedicle valve, BB 72511	7.2	13.5
Internal mould of pedicle valve, BB 72512	7.2	10.8
External mould of brachial valve, BB 72513	—	10.7

HORIZON AND LOCALITIES. All figured material from loc. 44, colln OA1. Also recorded from locs 46 and 48.

Leptestiina sp.

Figs 399, 403, 407, 408

DESCRIPTION. Subcircular *Leptestiina* with evenly concavo-convex horizontal profile, with pedicle valve about 60% as long as wide and 35% as deep as long, ventral interarea apscaline, pseudo-deltidium small and apical, dorsal interarea short, hypercline; ornament unknown.

Ventral interior with short blunt teeth supported by receding dental lamellae; ventral muscle field pentagonal in outline, extending anteriorly for about 30% of the length of the valve and 75% as long as wide, adductor field lanceolate, weakly impressed, diductor scars almost meeting anteriorly to surround diductor scar.

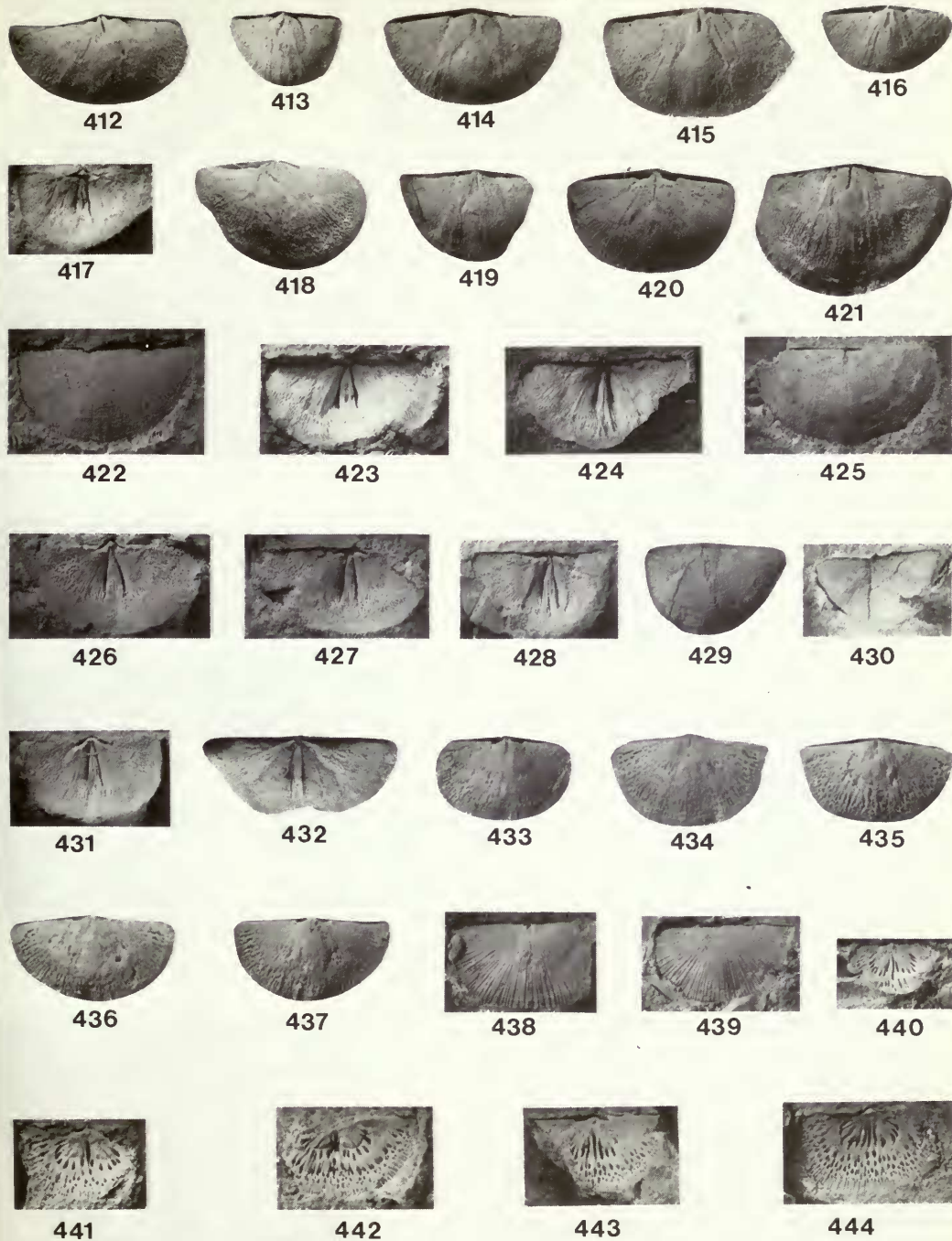
Dorsal interior with simple cardinal process consisting of anteriorly bifurcating, thin shaft connecting with notothyrial platform, socket ridges widely disposed subparallel to hinge defining a pair of oval sockets, lophophore platform 60% as long as wide, weakly defined posteriorly but apparently connecting with distal ends of socket ridges, medially incised anteriorly and ornamented by radiating ridges.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72514	2.4	5.2
Internal mould of pedicle valve, BB 72515	4.0	8.6
Internal mould of pedicle valve, BB 72516	5.7	9.8

HORIZON AND LOCALITIES. All figured material from loc. 47, colln CF1.

DISCUSSION. The few moulds of *Leptestiina* from the Acton Scott Formation show that there are two stocks present, which differ from each other in terms of outline, valve depth and ventral muscle field configuration. However, it is difficult to assess the importance of these differences until more is known about the variability of the stocks.

Figs 412–444 *Sowerbyella sericea* (J. de C. Sowerby), internal moulds of pedicle valves: 412 = BB 73590, $\times 2$, 413 = BB 73591, $\times 1.8$, 414 = BB 73592, $\times 2$, 415 = BB 73593, $\times 1.9$, 416 = BB 73602, $\times 1.9$, 418 = BB 73601, $\times 1.6$, 419 = BB 73604, $\times 2$, 420 = BB 73603, $\times 2$, 421 = BB 73600, $\times 2$; internal moulds of brachial valves: 417 = BB 73607, $\times 1.8$, 423 = BB 73608, $\times 1.9$, 424 = BB 73606a, $\times 1.8$, 426 = BB 73597, $\times 1.8$, 427 = BB 73598, $\times 2$, 428 = BB 73595a, $\times 1.4$, 431 = BB 73609, $\times 1.8$, 432 = BB 73594, $\times 1.7$; external moulds of brachial valves: 422 = BB 73599, $\times 1.8$, 425 = BB 73606b, $\times 1.9$, 429 = BB 73595b, $\times 1.6$, 430 = BB 73596, $\times 1.6$. *Chonetoides radiatula* (Barrande), internal moulds of pedicle valves: 433 = BB 73568, $\times 3$, 434 = BB 73565, $\times 3.5$, 435 = BB 73566, $\times 3$, 436 = BB 73569, $\times 3.7$, 437 = BB 73567, $\times 3.6$; external moulds of brachial valves: 438 = BB 73576, $\times 3.6$, 439 = BB 73577, $\times 3.2$; internal moulds of brachial valves: 440 = BB 73575, $\times 2.7$, 441 = BB 73573, $\times 3.8$, 442 = BB 73574, $\times 3$, 443 = BB 73572, $\times 3.2$, 444 = BB 73571, $\times 3.5$.



Family **SOWERBYELLIDAE** Öpik, 1930
Subfamily **SOWERBYELLINAE** Öpik, 1930

Genus **SOWERBYELLA** Jones, 1928

Sowerbyella sericea (J. de C. Sowerby)

Figs 412–432

- 1839 *Leptaena sericea* J. de C. Sowerby in Murchison : 636; pl. 19, fig. 1.
1928 *Sowerbyella sericea* (J. de C. Sowerby) Jones : 414; pl. 21, figs 1–4.
1963 *Sowerbyella sericea* (J. de C. Sowerby); Williams : 430–432; pl. 11, figs 1–9.
1970 *Sowerbyella sericea* (J. de C. Sowerby); Bretsky : 85–87; pl. 12, figs 3–6; pl. 13, figs 1–4.
cf. 1974 *Sowerbyella sericea* (J. de C. Sowerby); Williams : 134–135; pl. 24, figs 11–14, 16.

REMARKS. Williams (1963) redescribed and refigured *S. sericea*, based on material from the Alternata Limestone Formation exposed at Soudley Quarry (loc. 7), and it is in no need of revision here. The species is common throughout the Cheney Longville Formation and has been recorded from locs 1 to 33 inclusive, 35, 46 and 47. The specimens figured are derived from the Cheney Longville Formation, selected to give some idea of the variability of this widespread and common stock. Of the figured material BB 73590–1, BB 73594, BB 73595a, b and BB 73596 are from loc. 15, colln W5; BB 73592–3, BB 73597–9 are from loc. 26, colln M15. The remainder come from loc. 25, colln WFT8.

Genus **EOPLECTODONTA** Kozłowski, 1929

Eoplectodonta cf. *rhombica* (M'Coy)

Figs 404–406, 409–411

- 1852 *Leptaena sericea* var. *rhombica* M'Coy : 239.
1928 *Sowerbyella rhombica* (M'Coy) Jones : 426–430; pl. 22, fig. 1.
cf. 1963 *Eoplectodonta* cf. *rhombica* (M'Coy) Williams : 448–451; pl. 12, figs 9–14, 18, 19.

DESCRIPTION. Subcircular *Eoplectodonta* with evenly convex longitudinal profile, cardinal angles slightly obtuse, pedicle valve about 50% as long as wide and 30% as deep as long; ventral interarea apscaline, apical pseudodeltidium small; radial ornamentation unknown.

Ventral interior with small elongate teeth, divergent, denticles often developed for over half of hinge line, ventral muscle field strongly impressed, deeply cordate in outline and about 70% as long as wide and extending anteriorly for about 50% of the valve length, small oval adductor scar separated by median ridge, diductor scars widely separated anteriorly.

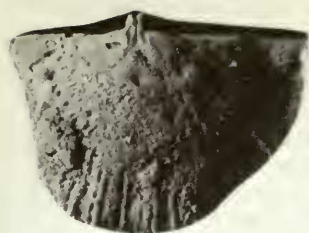
Dorsal valve unknown.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 72518	6·7	13·1
Internal mould of pedicle valve, BB 72519	6·4	13·1
Internal mould of pedicle valve, BB 72520	6·8	11·1
Internal mould of pedicle valve, BB 72521	4·3	11·4
External mould of brachial valve, BB 72522	5·7	11·6

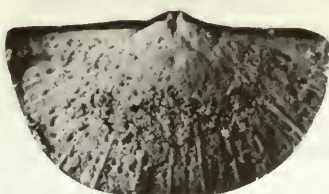
HORIZON AND LOCALITIES. All figured material is from loc. 41, colln O104. Also recorded from loc. 40.

DISCUSSION. The few ventral valves of *Eoplectodonta* recovered from the upper Acton Scott Formation of the Onny Valley are best compared with *E. cf. rhombica* described by Williams (1963)

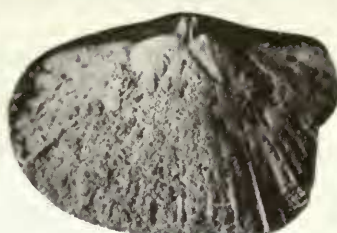
Figs 445–456 *Sericoidea homolensis* Havlíček, internal moulds of pedicle valves: 445 = BB 73581, ×9, 446 = BB 73582, ×12·5, 447 = BB 73578, ×11, 448 = BB 73580, ×11, 449 = BB 73579, ×10·7; internal moulds of brachial valves: 450 = BB 73586, ×11·4, 451 = BB 73584, ×13, 452 = BB 73586, ×11·5, 453 = BB 73583, ×10·7, 454 = BB 73587, ×11; external moulds of brachial valves: 455 = BB 73589, ×11·8, 456 = BB 73588, ×11·7.



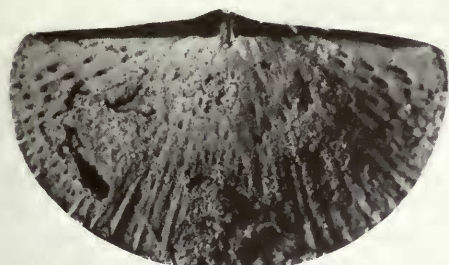
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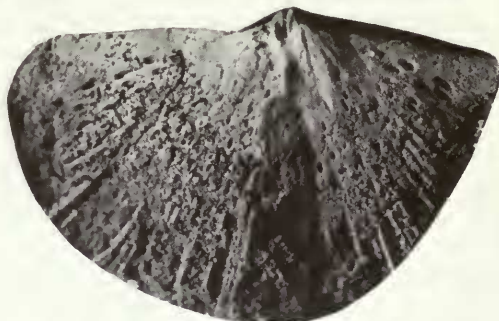
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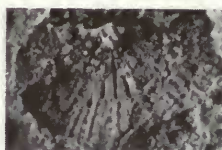
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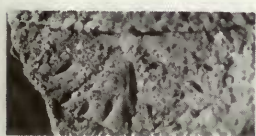
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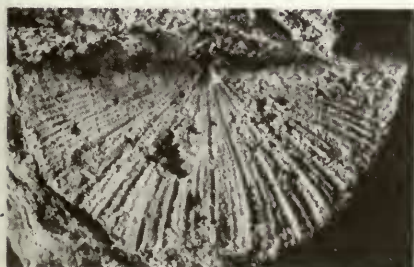
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456

from the Gelli-grin Calcareous Ashes (Longvillian) of the Bala district. They are alike in valve and muscle field outline and particularly in the suppression of rugae.

Subfamily AEGIROMENINAE Havlíček, 1961

Genus *CHONETOIDEA* Jones, 1928

Chonetoidea radiatula (Barrande)

Figs 433–444

- 1879 *Chonetes radiatulus* Barrande : pl. 54, fig. 1, 1–17.
 1952 *Chonetoidea radiatula* (Barrande) Havlíček : 405; pl. 3, fig. 8.
 1967 *Chonetoidea radiatula* (Barrande); Havlíček : 49; pl. 5, figs. 7–14.
 1977 *Chonetoidea radiatula* (Barrande); Mitchell : 93–94; pl. 18, figs 20–36.

DESCRIPTION. Transversely semicircular concavo-convex *Chonetoidea* 60% as long as wide and 15% as deep as long; rectangular cardinal angles with maximum width at hinge, ventral interarea apscaline and possibly with apical pseudodeltidium, dorsal interarea hypercline; ornament finely costellate occasionally with accentuated rib.

Ventral interior with small cordate diductor muscle scar about 30% as long as the valve and 40% as wide as valve length; median oval diductor muscle scar weakly impressed, teeth small, blunt with receding supports, occasional nodes occurring along the hinge line; papillose interior.

Dorsal interior with narrow socket ridges slightly divergent to hinge line and medially ankylosed to ridge-like cardinal process which is produced posteriorly into a trifid head; lophophore platform with strong median septule and up to 7 or 8 strong side septules arranged in an arc at about valve mid-length; adductor muscle field weakly impressed immediately adjacent to inside of median septule.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 73565	4.5	6.7
Internal mould of pedicle valve, BB 73566	4.5	7.5
Internal mould of pedicle valve, BB 73567	3.5	7.3
Internal mould of pedicle valve, BB 73568	3.7	6.7
Internal mould of pedicle valve, BB 73569	3.5	6.4
Internal mould of brachial valve, BB 73571	4.0	6.6 (est.)
External mould of brachial valve, BB 73576	3.9	7.3 (est.)
External mould of brachial valve, BB 73577	3.6	6.2

HORIZON AND LOCALITIES. All figured specimens are from loc. 46, colln AS6. Also recorded from locs 34–45 inclusive.

DISCUSSION. See p. 281.

Genus *SERICOIDEA* Lindström, 1953

Sericoidea homolensis Havlíček

Figs 445–456

- 1928 *Chonetoidea* ? sp. 2 Jones : 502.
 1967 *Sericoidea homolensis* Havlíček : 52–53; pl. 8, figs 1–5.

DESCRIPTION. Transverse semicircular concavo-convex *Sericoidea* 65% as long as wide and 20% as deep as long, maximum width at hinge, ventral interarea apscaline and medially with convex pseudodeltidium, dorsal interarea weakly hypercline to catacline; ornament parvicostellate with bundles of 2 or 3 ribs.

Ventral interior with small, weakly impressed cordate diductor muscle field about 25% as long and 40% as wide as the valve length, adductor scars not known, teeth very short, blunt and divergent, almost parallel with hinge line; finely papillose interior.

Dorsal interior with thin socket ridges subparallel to hinge and united medially with ridge-like

cardinal process which has a trifid head; lophophore platform with median septule and up to 5 or 6 often weakly developed lateral septules arranged in an arc at about 65% valve length, adductor scars not known.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 73578	2.9	4.3
Internal mould of pedicle valve, BB 73579	4.0	6.0
Internal mould of pedicle valve, BB 73580	3.0	5.5
Internal mould of pedicle valve, BB 73581	3.4	5.0
Internal mould of pedicle valve, BB 73582	2.1	3.7
Internal mould of brachial valve, BB 73585	3.2	5.1
Internal mould of brachial valve, BB 73586	1.9	2.7
External mould of brachial valve, BB 73588	2.5	5.3
External mould of brachial valve, BB 73589	2.7	4.5

HORIZON AND LOCALITIES. All figured specimens are from the Onny Shale Formation, loc. 50, colln O36. Also recorded from locs 49 and 51.

DISCUSSION. According to Mitchell (1977 : 93) the distinction between *Chonetoidea* and *Sericoidea* is based primarily on the former having fine canals penetrating the ventral interarea, usually preserved as small nodes (see Cocks 1970) and finely costellate as opposed to parvicostellate ribbing. The presence of nodes has only been noted with certainty in *C. radiatula*; an occasional specimen of *S. homolensis* may have them, however, although the evidence is equivocal owing to the poor preservation. Ribbing patterns are also variable and it is not impossible, given larger and better-preserved collections, that all gradations between the two may be found in one population. Certainly there seems to be a stratigraphical trend from *Chonetoidea* to *Sericoidea* type ribbing patterns predominating in a population, but again owing to the lack of well-preserved material (and lack of outcrop) it is not known if the gradation is disjunct or continuous. Although the two genera are here kept separate pending a comprehensive taxonomic treatment based on large populations traced through continuous sections, it is felt that *Sericoidea* may prove to be a synonym of *Chonetoidea*.

C. radiatula from the type Caradoc agrees in all morphological details with topotype material (Havlíček 1967). In terms of septule arrangement it closely resembles *C. stoermeri* from the Ordovician of the Oslo region (Spjeldnaes 1957).

S. homolensis appears to be the *Sericoidea* with the most complex septule arrangement; cf. *S. restricta* (Lindström 1953) and *S. abdita* (Whittington & Williams 1955). The Caradoc specimens agree with the Bohemian species *S. homolensis* in all aspects of morphology.

Jones (1928) had at his disposal the internal mould and cast of a single pedicle valve from the Onny Shale collection of Reynolds. He doubtfully assigned this to *Chonetoidea*, but although he did not figure it, it probably belongs to *S. homolensis* on stratigraphical grounds.

Superfamily **STROPHOMENACEA** King, 1846

Family **STROPHOMENIDAE** King, 1846

Subfamily **STROPHOMENINAE** King, 1846

Genus **STROPHOMENA** de Blainville, 1825

Strophomena grandis (J. de C. Sowerby)

Figs 457–466

1839 *Orthis grandis* J. de C. Sowerby in Murchison : 638; pl. 20, figs 12, 13.

1933 *Longvillia grandis* (J. de C. Sowerby) Bancroft : 3.

1963 *Strophomena grandis* (J. de C. Sowerby) Williams : 452–453; pl. 12, figs 17, 20, 21; pl. 13, fig. 2.

DISCUSSION. Williams (1963) redescribed and refigured *S. grandis* but in doing so he redefined the species based on moulds from the *Dalmanella watti* beds (Bancroft 1945) of Marshwood Quarry (loc. 27). My extensive collections indicate that *S. grandis* is very rare at this horizon, being far

more abundant in the overlying *D. unguis* beds. However, at Marshwood Quarry almost all the exposure of the *D. watsi* beds is represented by what Bancroft (1929a) referred to as the *Heterorthis praeculta* beds, which are now included in the *D. watsi* beds, and represent a faunal and sedimentary facies transition between the *D. watsi* and *D. unguis* beds.

Within the topmost strata of the *D. watsi* beds (= *H. praeculta* beds) *S. grandis* occurs sparingly, and it is from this horizon that Williams probably obtained his *S. grandis* material which is morphologically indistinguishable from *S. grandis* in the overlying *D. unguis* beds. However, below the *H. praeculta* horizon of the *D. watsi* beds very rare *Strophomena* occur which for the present are referred to *S. grandis* until more is known about the variability of the stock. The few specimens available for study appear to differ from typical *S. grandis* in being more transverse, finer-ribbed (5 or 6 costellae per mm, 10 mm anteromedially of the dorsal umbo) and in having a less impressed ventral muscle field.

DIMENSIONS.	length	width
Internal mould of brachial valve, BB 73533	30.1	46.8
Internal mould of brachial valve, BB 73534	34.5	42.3
Internal mould of brachial valve, BB 73535	25.2	—
Internal mould of pedicle valve, BB 73537	28.2	40.8
Internal mould of pedicle valve, BB 73538	26.2	36.8
Internal mould of pedicle valve, BB 73539	26.1	38.0
Internal mould of pedicle valve, BB 73540	23.3	39.9

HORIZON AND LOCALITIES. BB 72533–8 inclusive are from loc. 24, colln WFT1 of the *D. unguis* beds. BB 73539 (loc. 27, colln M1), BB 73540 (loc. 19, colln CL2), BB 72541–2 (loc. 32, collns LM4 and LM1 respectively) are from the *D. watsi* beds of Bancroft (1933). Also recorded from locs 21, 23, 26 and 28–33.

Subfamily RAFINESQUININAE Schuchert, 1893

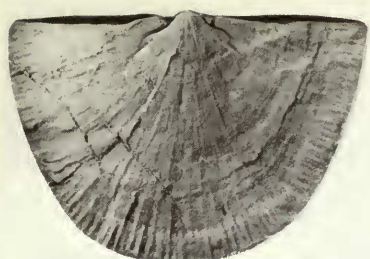
Genus *KJAERINA* Bancroft, 1929

DIAGNOSIS (emended). Elongately triangular to semicircular alate strophomenides, with weakly to moderately strongly convex, dorsally geniculate pedicle valve and plane to anteriorly weakly dorsally geniculate brachial valve, skirt short and rounded, gently angulate, geniculate specimens with semicircular disc; ornamented by unequal parvicostellae and with very prominent medial rib, and posterolaterally along hinge with very fine irregular rugae; ventral interarea apscaline with vestigial pseudodeltidium; dorsal interarea anacline medially with small convex grooved chilidium; finely pseudopunctate.

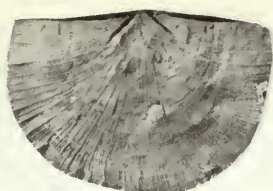
Ventral interior with short, squat, obliquely-placed teeth bisecting angle between hinge and receding dental plates which support them; dental plates narrowly divergent, extending anteriorly as low ridges laterally bounding ventral muscle field, ventral muscle scar narrow, triangular medially, with a lanceolate adductor scar on a shallow platform which is sometimes completely surrounded by diductor tracks.

Dorsal interior with delicate cardinalia consisting of a small splayed cardinal process posteriorly ankylosed to narrowly divergent socket ridges, notothyrial platform often strongly developed, anchor-shaped, bounding oval hollows of posterior adductors, rounded shallow medial ridge separating adductors.

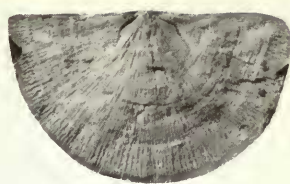
Figs 457–476 *Strophomena grandis* (J. de C. Sowerby), internal moulds of pedicle valves: 457 = BB 73537, $\times 1.2$, 458 = BB 73539, $\times 0.9$, 459 = BB 73540, $\times 0.9$, 461 = BB 73541, $\times 0.8$, 462 = BB 73538, $\times 0.8$, 463 = BB 73536, $\times 0.8$; internal moulds of brachial valves: 460 = BB 73535, $\times 1.2$, 464 = BB 73542, $\times 1.1$, 465 = BB 73533, $\times 1.2$, 466 = BB 73534, $\times 1.1$. *Kjaerina bipartita* (Salter), internal moulds of pedicle valves: 467 = BB 73558, $\times 1.2$, 468 = BB 73557, $\times 0.9$, 469 = BB 73556, $\times 1.3$, 470 = BB 73554, $\times 1.1$, 471 = BB 73555, $\times 1.1$, 472 = BB 73559a, $\times 1.5$; internal moulds of brachial valves: 474 = BB 73562, $\times 1.5$, 475 = BB 73561, $\times 1.2$, 476 = BB 73560, $\times 1.3$; external mould of pedicle valve: 473 = BB 73559b, $\times 1.3$.



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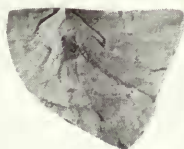
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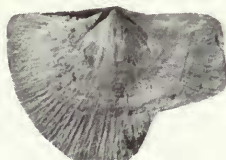
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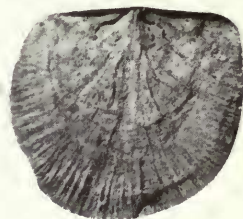
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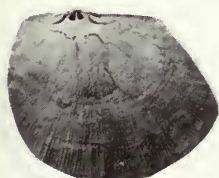
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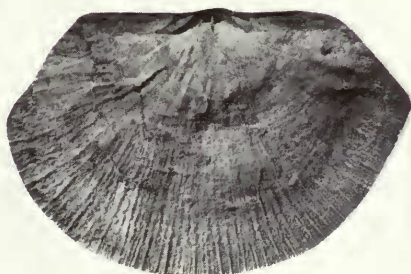
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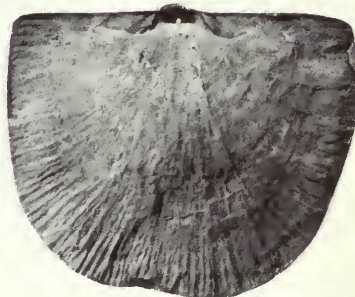
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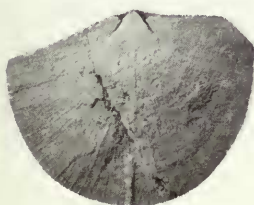
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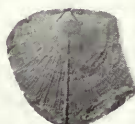
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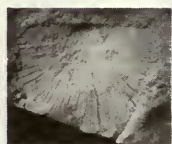
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TYPE SPECIES. *Kjaerina tya* Bancroft, 1929, by original definition of Bancroft (1929a : 43).

DISCUSSION. The chequered taxonomic history of *Kjaerina* is closely related to that of *Hedstroemia* and is discussed under the latter genus, p. 287.

Kjaerina bipartita (Salter)

Figs 467–473

1854 *Strophomena bipartita* Salter : 74.

1929a *Kjaerina bipartita* (Salter) Bancroft : 52–53; pl. 1, fig. 14.

1945 *Kjaerina bipartita* (Salter); Bancroft : 248–249; pl. 37, figs 3–4.

1958 *Kjaerina bipartita* (Salter); Dean : pl. 24, fig. 19.

1978 *Kjaerina bipartita* (Salter); Cocks : 112.

DESCRIPTION. Semicircular, gently plano-convex *Kjaerina*, with a pedicle valve about 80% as long as wide and evenly convex, brachial valve plane with rectangular cardinal angles, ventral interarea apscaline, pseudodeltidium vestigial, dorsal interarea anacline, chilidium small, arched and only covering dorsal end of cardinal process lobes, radial ornamentation unequally parvicostellate with commonly 4 costellae per mm, 10 mm anteromedially of ventral umbo, and always with strongly accentuated median rib.

Ventral interior with very small teeth oblique to hinge line and fused to short receding dental lamellae which extend forward for 15% of the valve length, ventral muscle field rounded triangular, faintly impressed, as wide as long and 25% as long as the valve with submedian lanceolate adductor scar occasionally surrounded by diductor tracks.

Dorsal interior with short delicate cardinal process lobes ankylosed to narrowly divergent socket ridges which extend forward for about 10% of the valve length, notothyrial platform and median ridge faintly developed, posterior adductor scars faintly impressed.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 73555	22.4 (est.)	30.4 (est.)
Internal mould of pedicle valve, BB 73556	10.2	14.2 (est.)
Internal mould of pedicle valve, BB 73557	13.5 (est.)	14.3 (est.)
Internal mould of pedicle valve, BB 73558	22.0	27.4
Internal and external mould of pedicle valve, BB 73559a, b	12.3	14.7

HORIZON AND LOCALITIES. BB 73554–5 and BB 73562 from loc. 17, colln S9; BB 73556–8 and BB 73561 from loc. 17, colln S7; BB 73559a, b and BB 73560 from loc. 1, colln CL9. Also recorded from locs 2–8, 13, 14 and 16.

DISCUSSION. See p. 286.

Kjaerina tya Bancroft

Figs 477–498

1929a *Kjaerina tya* Bancroft : 53–54; pl. 1, fig. 15.

1929a *Kjaerina geniculata* Bancroft : 54–55; pl. 1, figs 16–17.

1945 *Kjaerina geniculata* Bancroft; Bancroft : 249–256; pl. 37, figs 5–7.

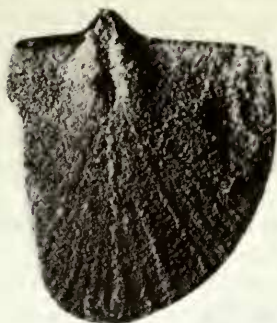
1958 *Kjaerina tya* Bancroft; Dean : pl. 24, fig. 20.

DESCRIPTION. Elongately semicircular to triangular, gently plano-convex to concavo-convex,

Figs 477–498 *Kjaerina tya* Bancroft, internal moulds of pedicle valves: 477 = BB 73626, $\times 11.5$, 478 = BB 73627, $\times 9.5$, 479 = lectotype BB 14383, $\times 1.5$, 480 = BB 73637, $\times 0.8$, 481 = BB 73628, $\times 3.1$, 482 = BB 73630, $\times 0.8$, 483 = BB 73631, $\times 1$, 484 = BB 73632, $\times 0.8$, 485 = BB 73636, $\times 0.8$, 486 = BB 73633, $\times 0.9$, 487 = BB 73639, $\times 1$, 488 = BB 73635, $\times 0.9$, 489 = BB 73629, $\times 1.4$, 490 = BB 73634, $\times 1.2$, 491 = BB 73640, $\times 1.2$, 492 = BB 73638, $\times 1.2$; internal moulds of brachial valves: 493 = BB 73645, $\times 1.1$, 494 = BB 73644, $\times 1.1$, 495 = BB 73641, $\times 10.8$, 496 = BB 73646, $\times 1.9$, 497 = BB 73642, $\times 1.7$, 498 = BB 73643, $\times 4$.



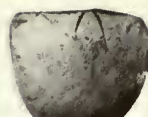
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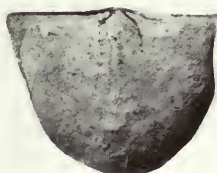
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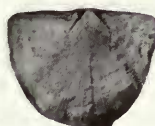
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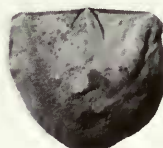
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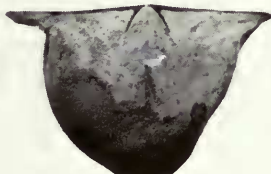
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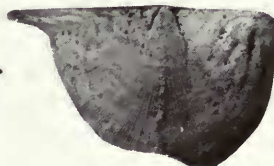
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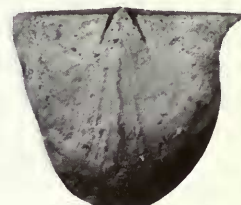
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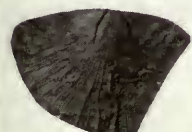
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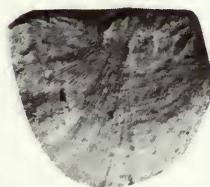
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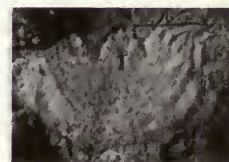
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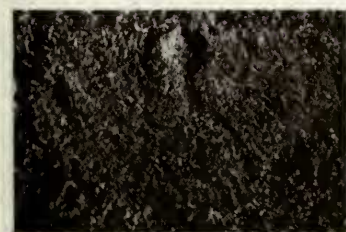
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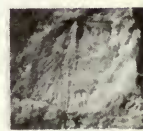
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weakly to strongly dorsally geniculate alate *Kjaerina*, with a pedicle valve about 75% as long as wide, initially weak to moderately convex becoming plane anteriorly; valve gently geniculate, trail approximately up to 30% as long as valve length; disc if present oval and covered with posterolateral impersistent, weak rugae; ventral interarea apscaline, pseudodeltidium appearing absent, dorsal interarea anacoline with small arched chilidium; radial ornamentation unequal parvicostellate, commonly with 4 ribs per mm, 10 mm anteromedially of the ventral umbo.

Ventral interior with small stubby teeth acute to hinge line and supported by narrowly divergent receding dental lamellae extending forward for about 10% of the valve length; muscle field as broad as long and extending forward for 50% of the valve length and bounded laterally by shell ridges extending from dental plates, submedian adductor scar raised on small platform and occasionally with transmuscle septa; diductor tracks may completely surround adductor tracks.

Dorsal interior with small, delicate, bilobed cardinal process posteriorly ankylosed to weakly divergent socket ridges which extend anteriorly for approximately 20% of the valve length, notothyrial platform weakly to strongly developed, anchor-shaped, shallow median ridge separating small posterior adductor muscle impressions.

ONTOGENY. Collection O110 from loc. 12, the type locality for *K. typa*, afforded numerous small individuals of both valves allowing an ontogenetic series for the species to be established. The pedicle valves of small individuals (c. 2 mm wide) are characterized by a massive bulbous convex protegular node with relatively thick teeth and dental plates fused to it posteriorly. There is already differentiation of the diductor and adductor tracks, and the strong median rib so characteristic of *Kjaerina* is already established (Fig. 477), and penetrates into the node. With growth the node is consumed in the ventral muscle field and assumes a more triangular shape. The teeth and dental plates decrease relatively in size and by 4 or 5 mm in size (width) individuals have attained adult characteristics (Fig. 481). With brachial valves, initially (valve width c. 2.5 mm wide) the protegular node is a convex Y shape with the median ridge and socket plates fused to it anteriorly and laterally, whilst posteriorly a small bilobed cardinal process is also attached to it. With growth the node differentiates and by 4 mm valve width the adult characters are present.

MATERIAL AND LOCALITIES. Lectotype (Fig. 479) BB 14383 (selected Cocks 1978 : 113), est. length 22.3 mm, est. width 25.2 mm, from loc. 12. Also from loc. 12 (colln O110) BB 73626 (Fig. 477), length 1.8 mm, width 2.0 mm; BB 73627 (Fig. 478), length 3.4 mm, width 4.8 mm; BB 73628 (Fig. 481), length 3.7 mm, width 5.0 mm; BB 73641 (Fig. 495); BB 73643 (Fig. 498); BB 73642 (Fig. 497), and from colln O22 BB 73638 (Fig. 492), length 19.9 mm, est. width 22.7 mm, and colln O113 BB 73639 (Fig. 487), length 22.4 mm and BB 73640 (Fig. 491). Also from loc. 9, with more than 24 individuals on one slab, including BB 73629–37 (Figs 480, 482–6, 488–90) and BB 73644–6 (Figs 493–4, 496), and locs 10, 11, 15 and 18, all from the Glynboro Member of the Cheney Longville Formation.

DISCUSSION. Bancroft (1929a) proposed ten new species in his genus *Kjaerina*. Two of these, *K. typa* and *K. geniculata*, as well as *K. bipartita* (Salter), occur in the upper Caradoc.

The type locality for *K. bipartita* is ambiguous. Salter (1854) reported the shells to be found near Hope Bowdler, Cheney Longville and in thin flags of the Horderley section. Bancroft (1929a : 52) assumed that this meant that the species was based on material from the middle part of the Alternata Limestone of Cheney Longville. Thus, in his erection of *Kjaerina* species, *K. bipartita* is based on material from this horizon. From the description of Salter in finding *K. bipartita* in thin flags (which presumably indicates the presence of parallel laminae), the material is most likely to derive from the Alternata Limestone or lower Cheney Longville Formation.

Based on material from the Alternata Limestone Formation and lowest Cheney Longville Formation of the Caradoc district (note that Salter indicated the species to occur throughout the district), *K. bipartita* differs from other upper Caradoc *Kjaerina* in its weakly plano-convex shell, lack of posterolateral rugae, faintly impressed ventral muscle areas, small teeth and receding dental plates and semicircular outline.

K. geniculata is very rare at the type locality (loc. 10 of this report) but a large topotype population of *K. typa* was obtained (loc. 12 of this report) and the morphological variation expressed by

this population encompasses *K. geniculata* in every respect. Perhaps the most striking difference between the two species, according to Bancroft's descriptions, was the dorsal geniculation of *K. geniculata*. However, this is a continuously variable character and end members of *K. typa* variation series are also geniculate. Contrary to the assertions of Bancroft, geniculation also affects brachial valves (Figs 493–8). It should also be noted that Bancroft (1929a : 54) admitted that 'it is thus a matter of considerable embarrassment to know where to draw the line between different species'. Here he was talking about the difficulties of separating *K. typa* from *K. geniculata*, though in all fairness it should be stated that he was more concerned with the stratigraphical subdivision.

In view of the close morphological similarity between the two species, *K. geniculata* is here synonymized with *K. typa*.

Genus *HEDSTROEMINA* Bancroft, 1929

DIAGNOSIS (emended). Weakly to strongly plano-convex to concavo-convex strophomenides, weakly to strongly dorsally geniculate with a weak anterior sulcus, skirt short to long and rounded to abruptly angulate with semirounded disc; ornamented by unequal parvicostellate ribs and often with prominent medial rib and very impersistent concentric wrinkles; ventral interarea apscaline with small to large apical foramen and vestigial or resorbed pseudodeltidium, dorsal interarea anacline to orthocline with convex, medially grooved chilidium; finely pseudopunctate.

Ventral interior with short, squat, obliquely-placed teeth, supported by short to long, thin to thick, narrowly to widely divergent dental plates which may extend forward to bound the muscle field laterally, ventral muscle scar wide, triangular to subcircular, often flabellate and posteriorly consisting of a submedian lanceolate adductor scar, sometimes on a platform of transmuscle septa and completely surrounded by diductor scars, lanceolate ventral adjustor scars parallel to dental plates.

Dorsal interior with delicate cardinalia consisting of a slightly splayed bilobed blade-like cardinal process ankylosed posteriorly to thin divergent socket ridges and anteriorly to slightly raised broad median ridge, notothyrial platform weakly to moderately developed as a raised anchor-shaped feature bounding shallow oval hollows corresponding to the attachment sites of the posterior adductors.

TYPE SPECIES. *Hedstroemina fragilis* Bancroft, 1929, by original designation of Bancroft (1929a : 56).

DISCUSSION. Bancroft erected *Hedstroemina* for a group of Marshbrookian and post-Marshbrookian concavo-convex, subgeniculate or dorsally geniculate rafinesquinids. In doing so he recognized the close similarity between *Hedstroemina* and *Kjaerina bipartita*, but stated that they could be distinguished by the geniculate or sharply flexed dorsal valve and the regular type of ribbing in *Hedstroemina*. However, the geniculation and deflection of the dorsal valve in *Hedstroemina* are highly variable features and specimens often resemble the geniculate *K. typa*. Further, the ribbing type of *Hedstroemina* is very similar to *Kjaerina*.

Salmon (1942 : 570–571) synonymized *Kjaerina* and *Hedstroemina* with *Rafinesquina*, believing them to be essentially the same stock. Spjeldnaes (1957 : 129–130) reported that the differences between the genera are concerned mainly with ventral musculature, geniculation and ribbing. He listed *Kjaerina* as having narrowly divergent ventral muscle impressions, a non-geniculate or only slightly geniculate ventral valve and always a flat dorsal valve. In contrast, *Hedstroemina* supposedly had widely divergent ventral muscle impressions and strongly dorsally geniculate valves. The extreme variability of such features led Spjeldnaes to regard the two genera simply as subgenera of *Rafinesquina*.

Williams *et al.* (1965) kept *Kjaerina* and *Rafinesquina* as separate genera, distinguishing between the two on the much stronger posterolateral rugae development of *Kjaerina* and also the low subparallel bounding ridges around a lightly impressed ventral muscle field. *Hedstroemina* was placed as a subgenus of *Kjaerina*, distinguished from it by its commonly strongly dorsally geniculate valves and rarity of thickened median costae.

Rafinesquina, *Kjaerina* and *Hedstroemina* are clearly all very close morphologically. However, the characters used by Williams *et al.* (1965) to distinguish between the *Kjaerina* group and *Rafinesquina* are applicable, since the two taxa can be consistently recognized by them. In this study *Hedstroemina* is consistently distinguished from *Kjaerina* by the following characteristics:

1. The convex and commonly strongly dorsally geniculate pedicle valve, and concave or weakly geniculate brachial valve
2. The wider, more impressed ventral musculature plus the common occurrence of trans-muscle septa
3. The more heavily calcified bilobed cardinal process
4. The less strongly developed median costae and the crinkly appearance (weak rugae ?) of the shell surface
5. Thinner socket ridges.

Hedstroemina fragilis Bancroft

Figs 499–515

1929a *Hedstroemina parva* Bancroft : 57–58; pl. 2, figs 4–5.

1929a *Hedstroemina fragilis* Bancroft : 58–59; pl. 2, figs 1–3.

1929a *Hedstroemina robusta* Bancroft : 59; pl. 2, figs 6–7.

cf. 1957 *Rafinesquina* (*Hedstroemina*) cf. *robusta* (Bancroft) Spjeldnaes : 133–134; pl. 8, fig. 5.

aff. 1957 *Rafinesquina* (*Hedstroemina*) aff. *robusta* (Bancroft) Spjeldnaes : 134–135; pl. 8, figs 1–4.

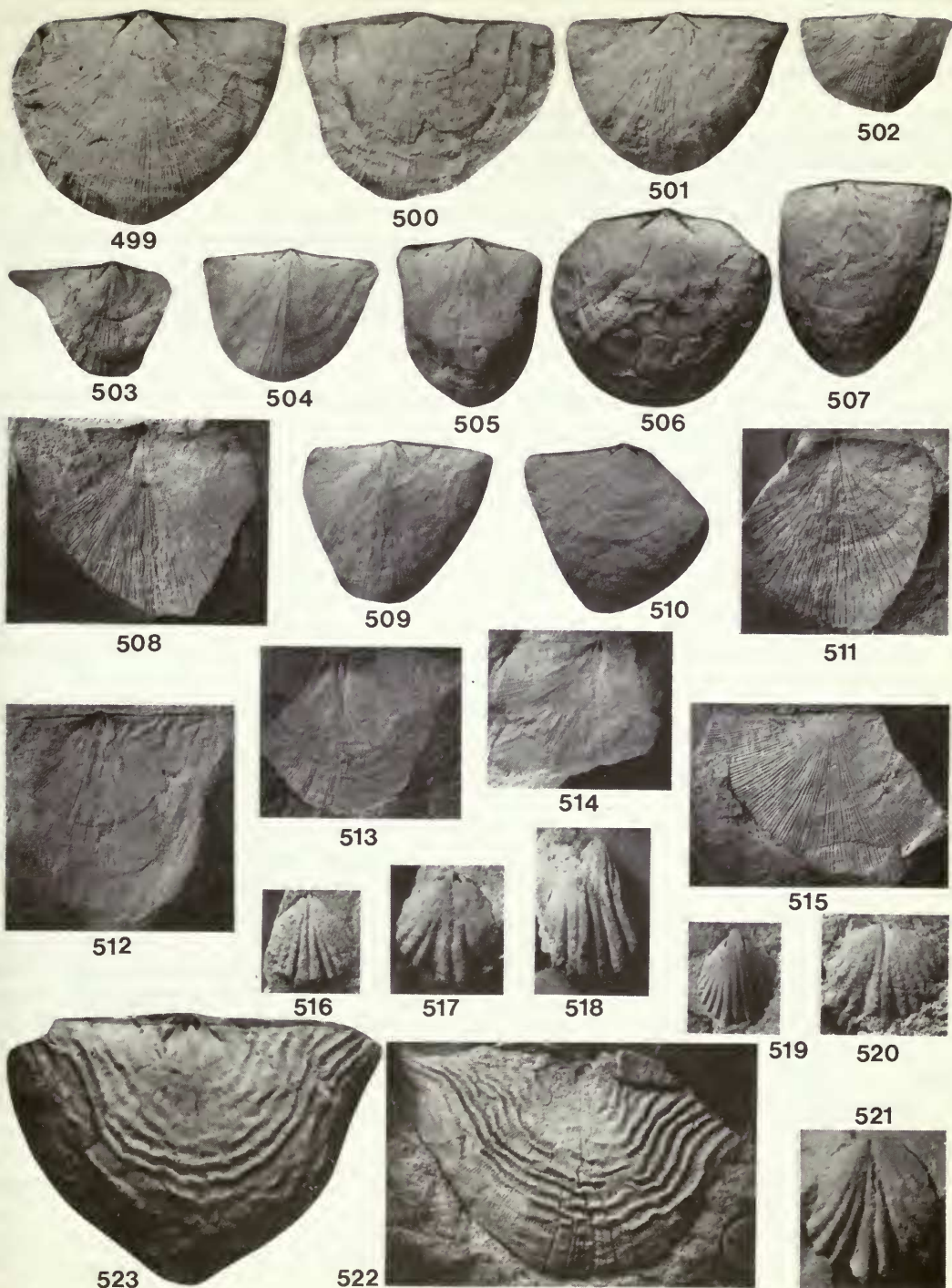
DESCRIPTION. Plano-convex to concavo-convex dorsally weakly to strongly geniculate *Hedstroemina*, semicircular in outline, 75% as long as wide, disc if present semicircular; shell surface covered by concentric wrinkles, ventral interarea apscaline and with small to large apical foramen and vestigial pseudodeltidium, dorsal interarea anacoline to orthocline with convex, medially grooved chilidium; radial ornamentation unequally parvicostellate, commonly with 5 ribs per mm, 10 mm anteromedially of the umbones.

Ventral interior with short stubby teeth placed to bisect angle between hinge and receding dental plates which support them and extend forward for about 18% of the valve length; ventral muscle field rounded triangular, somewhat flabellate and surrounded laterally by fine shell ridges, often as wide as long and extending forward for about 35% of the valve length, muscle field of larger specimens often traversed longitudinally by fine shell ridges.

Dorsal interior with blade-like, bilobed, splayed cardinal process ankylosed posteriorly to socket ridges which extend forward for about 20% of the valve length, anchor-shaped notothyrial platform well-developed in larger individuals, median ridge low and separating slightly etched posterior adductor scars.

MATERIAL AND LOCALITIES. Lectotype (Fig. 499) BB 14380 (selected Cocks 1978 : 112), length 22.0 mm, est. width 26.6 mm, from loc. 25, as is BB 73879 (Fig. 506), Bancroft colln, length 26.3 mm, width 27.0 mm, and (colln WFT7) BB 73545 (Fig. 502), length 10.5 mm, est. width 17.0 mm. Also from loc. 28, colln M12, e.g. BB 73551 (Fig. 512), BB 73552 (Fig. 514), BB 73553 (Fig. 505); loc. 43, colln CP2, e.g. BB 73543 (Fig. 507), BB 73544 (Fig. 503), and loc. 45, colln AS1,

Figs 499–523 *Hedstroemina fragilis* Bancroft, internal moulds of pedicle valves: 499 = lectotype BB 14380, $\times 1.5$, 500 = lectotype of synonymized *H. robusta* BB 14384, $\times 1.5$, 501 = lectotype of synonymized *H. parva*, BB 14385, $\times 1.5$, 502 = BB 73545, $\times 1.4$, 503 = BB 73544, $\times 1.1$, 504 = BB 73546, $\times 1.1$, 505 = BB 73553, $\times 0.8$, 506 = BB 73879, $\times 1.2$, 507 = BB 73543, $\times 0.8$, 509 = BB 73547a, $\times 1.3$, 510 = BB 73548a, $\times 1.4$; internal moulds of brachial valves: 512 = BB 73551, $\times 1.4$, 513 = BB 73932, $\times 1$, 514 = BB 73552, $\times 1$; external moulds of pedicle valves: 508 = BB 73547b, $\times 1.6$, 511 = BB 73548b, $\times 1.3$; external mould of brachial valve: 515 = BB 73550, $\times 1.4$. ? *Zygospira* sp., internal moulds of brachial valves: 516 = BB 72528, $\times 4$, 517 = BB 72525, $\times 3.7$, 520 = BB 72524, $\times 4$, 521 = BB 72526, $\times 4$; internal moulds of pedicle valves: 518 = BB 72527, $\times 3.2$, 519 = BB 72523, $\times 3.7$. *Kjerulfina polycyma* Bancroft, internal mould of brachial valve: 523 = BB 73901, $\times 1.1$; external mould of brachial valve: 522 = BB 73897, $\times 1.7$.



e.g. BB 73549–50 (Fig. 515). Loc. 47, Dean colln, e.g. BB 73546 (Fig. 504), BB 73547 (Figs 508–9), BB 73548 (Figs 510–1). Also from Dean colln, the old quarry, quarry field, Gretton, e.g. BB 73932 (Fig. 513). BB 14385 (Fig. 501) is lectotype of *parva* and is from Upper Barn, Wistanstow. Also known from locs 22, 27, 34–42, 44, 46 and 47, all in the upper Cheney Longville Formation and Acton Scott Formation.

DISCUSSION. Bancroft (1929a) erected three species of *Hedstroemina*, *H. parva*, *H. fragilis* and *H. robusta*. His descriptions were based only on ventral valves for *H. parva*, 'invariably much buckled and fractured' specimens of *H. fragilis*, and for *H. robusta* he concluded 'the material for this species is very poor' (Bancroft 1929a : 57–59).

H. fragilis is by far the most common species, a fact noted by Bancroft. Analysis of the variation expressed by the topotype population indicates a wide range, but one in which all the morphological characters are linked by a continuous morphological gradient. For instance, almost plane shells are linked continuously to strongly convex geniculated types. The variation expressed by this topotype population of *H. fragilis* completely encompasses the other two species; *H. parva* and *H. robusta* are therefore synonymized with *H. fragilis*.

Genus *KJERULFINA* Bancroft, 1929

DIAGNOSIS (emended). Weakly concavo-convex, ventrally geniculate, anteriorly weakly sulcate semicircular strophomenides with a triangular disc; ornamented by unequal parvicostellae and fine concentric growth lines, disc ornamented by fine to coarse irregular rugae; ventral interarea apscaline with small supra-apical foramen and resorbed pseudodeltidium, dorsal interarea apscaline with very small convex chilidium; finely pseudopunctate.

Ventral interior with short, stubby, obliquely placed teeth supported by short, thin, receding dental plates, ventral muscle scar flabellate, elongately subquadrate in outline and consisting of a submedian lanceolate adductor scar bounded by fine ridges and completely surrounded by diductor scars, lanceolate ventral adjustor muscles parallel to the dental plates, whole muscle complex bounded by fine muscle ridges.

Dorsal interior with fairly delicate cardinalia consisting of a slightly splayed bilobed cardinal process posteriorly ankylosed to slightly divergent thin socket ridges; notothyrial platform poorly developed as a slightly raised feature bounding oval hollows corresponding to the attachment site of the posterior adductors, median ridge low and broad.

TYPE SPECIES. *Kjerulfina trigonalis* Bancroft, 1929, by original definition of Bancroft (1929a : 59).

DISCUSSION. Bancroft (1929a : 59) erected this genus to embrace shells with valves of leptaenoid shape, trigonal or subparabolic contour and with an abruptly geniculate ventrally deflected border. Certainly the abrupt ventral deflection is probably the most characteristic feature of the shell. Bancroft was perplexed by this character, which he thought detracted from placing the genus in a group with *Rafinesquina* (1929a : 60). He suggested that it might belong to the Orthotetinae of Waagen, an assignment he later confirmed (1945 : 250). Spjeldnaes (1957) placed *Kjerulfina* in the subfamily Strophomeninae King, 1946, along with *Rafinesquina*. He also expanded the generic diagnosis of *Kjerulfina* to include amongst other things forms lacking a ventrally deflected geniculation. He consequently experienced difficulty in distinguishing *Kjerulfina* from *Strophomena* and *Holtedahlinia*, and the criteria he used, e.g. outline of the ventral muscle field and attitude of the intermuscle ridges, are untenable.

Kjerulfina was placed in the subfamily Rafinesquininae Schuchert, 1893 by Williams *et al.* (1965), an assignment which is owing to its close similarity to *Rafinesquina* in all aspects except geniculation.

Kjerulfina trigonalis Bancroft

Figs 524–535, 538

1929a *Kjerulfina trigonalis* Bancroft : 61; pl. 2, figs 8–9.

DESCRIPTION. Gently concavo-convex ventrally geniculate *Kjerulfina*, semielliptical to semi-circular in outline and 70% as long as wide, larger individuals alate, pedicle valve initially convex,

10% as deep as shell width becoming plane anteriorly; valve abruptly geniculate, trail about 15% as long as shell width, disc rounded triangular in outline and surface covered with very irregular weak rugae; ventral interarea apscaline and with small supra-apical foramen, pseudodeltidium appears absent, dorsal interarea apscaline with small arched chilidium; radial ornamentation unequally parvicostellate, often with the median rib thickened and with usually 4 ribs per mm, 10 mm anterior of the dorsal umbo.

Ventral interior with short teeth parallel to the weakly divergent receding dental plates which extend forward for 5% of the valve length; ventral muscle field elongately subquadrate and flabellate, surrounded by fine ridges extending anteriorly from dental plates, 66% as wide as long and extending forward for 40% of the length of the valve, fine ridges defining a median lanceolate adductor scar which is surrounded anteriorly by the adductor scars.

Dorsal interior with delicate elliptical bilobed cardinal process which is slightly splayed and ankylosed posteriorly to divergent thin socket ridges reaching anteriorly for 14% of the length of the brachial valve, notothyrial platform weakly developed, anchor-shaped, median ridge low and broad.

MATERIAL AND LOCALITIES. Lectotype (Fig. 524) BB 73834 (selected Cocks 1978 : 110), est. length 23.3 mm, est. width 38.0 mm, from loc. 27, also (colln M4) BB 72542 (Fig. 532), length 21.0 mm, width 26.6 mm. Also loc. 24, colln WFT1, e.g. BB 72539 (Figs 525–6), length 19.9 mm, width 33.0 mm; BB 72541 (Figs 530–1), length 20.3 mm, width 27.4 mm; loc. 20, colln O81, e.g. BB 72540 (Figs 528–9), length 18.5 mm; BB 72543 (Fig. 534). Loc. 11, Bancroft colln, e.g. BB 73928 (Fig. 533); loc. 20, Bancroft colln, e.g. BB 73913–4 (Figs 535, 538); loc. 31, e.g. BB 72538 (Fig. 527). Also recorded from locs 19, 26 and 30.

DISCUSSION. See p. 292.

Kjerulfina polycyma Bancroft
Figs 522, 523, 536, 537, 539–541

1929a *Kjerulfina polycyma* Bancroft : 61–62; pl. 2, figs 10–12.

1945 *Kjerulfina polycyma* Bancroft; Bancroft : 250–252; pl. 38, figs 1–5.

cf. 1952 *Kjerulfina* cf. *polycyma* Bancroft; Reed : 50; pl. 2, figs 6–7.

1957 *Kjerulfina limbata* Spjeldnaes : 156–157; pl. 9, figs 4, 9–10.

cf. 1977 *Kjerulfina* cf. *polycyma* Bancroft; Mitchell : 100–101; pl. 21, figs 7–10.

1978 *Kjerulfina polycyma* Bancroft; Harper & Boucot : pl. 14, figs 1–3, 5–9, *non* figs 4, 12.

DESCRIPTION. Plano-convex to gently concavo-convex ventrally geniculate *Kjerulfina*, elongately semicircular in outline, 65% as long as wide, occasionally larger individuals with an alate hinge line, pedicle valve initially gently convex, 12% as deep as wide, valve abruptly geniculate ventrally and trail 30% as long as valve is wide, disc semicircular in outline and surface covered with strong persistent rugae, ventral interarea apscaline with supra-apical foramen, pseudodeltidium appearing absent, dorsal interarea apscaline and with small vestigial arched chilidium; radial ornamentation unequally parvicostellate and often with median rib thickened and commonly with 5 ribs per mm, 10 mm anterior of the dorsal umbo.

Ventral interior with very short thickened teeth dividing angle between hinge and short receding dental plates which support them and extend forward for 10% of the valve length, ventral muscle field subquadrate, flabellate, and surrounded laterally by muscle-bounding ridges extending forward from dental plates and 85% as wide as long and extending forward for 40% of the length of the valve, median lanceolate adductor scars defined by small ridges and surrounded anteriorly by diductor tracks.

Dorsal interior with moderately strong, splayed, bilobed cardinal process ankylosed posteriorly to thin weakly divergent socket ridges which reach anteriorly for 12% of the length of the brachial valve, notothyrial platform moderately developed and anchor-shaped, median ridge fine.

DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 9148, lectotype	—	—
Internal mould and cast of pedicle valve, BB 73908	23.6	34.5
Internal mould of pedicle valve, BB 73895	21.5	32.2
Internal mould of pedicle valve, BB 73887	22.6 (est.)	26.5 (est.)
Internal mould of brachial valve, BB 73901	23.9	31.0
External mould of pedicle valve, BB 73897	19.7 (est.)	38.2 (est.)

HORIZON AND LOCALITIES. All figured specimens are from the Bancroft collection in the BM(NH). BB 73908 is from loc. 28; the rest are from loc. 25. Also recorded from loc. 22.

DISCUSSION. Bancroft (1929a, 1945) distinguished between *K. trigonalis* and *K. polycyma* on the basis of rugae, ventral disc, axis of geniculation, posterolateral wings and ventral muscle area. He considered *K. trigonalis* to have finer discontinuous rugae, a flat as opposed to a uniformly convex ventral disc, a narrow and rounded as opposed to a wide, steep and abruptly angulate geniculate border. He thought that *K. polycyma* did not develop alae (independent wings) and supposedly had a shorter and relatively wider ventral muscle field, bounded by finer ridges.

The present study indicates that *K. trigonalis* does indeed have much finer, more discontinuous rugae. However, a population of *K. polycyma* exhibits striking variation and a few individuals have rugae scarcely stronger than *K. trigonalis* (see Bancroft 1945 : 250). There is no obvious consistent difference in the convexity of the ventral disc. As regards the geniculate borders, *K. polycyma* populations do have consistently wider, steeper and more angulate trials. Alae seem to be persistently present in *K. trigonalis*, but occur only occasionally in *K. polycyma*. Perhaps the most striking difference between the two species is concerned with the ventral muscle field and cardinalia. *K. polycyma* has a consistently wider muscle area giving the whole field a quadrate appearance, but has weaker bounding ridges. Its teeth are stubbier and displayed at a more acute angle to the hinge axis than in *K. trigonalis*. Further, the dental plates are weaker and displayed at a wider angle. The notothyrial platform of *K. polycyma* is more strongly developed and its external ribbing appears to be slightly finer.

Spjeldnaes (1957) erected *K. limbata*, noting that it was closely related to *K. polycyma* but differed in terms of size and ventral muscle impression. Size is an unreliable taxonomic character and the ventral muscle configuration and impression are accommodated within the range of variation of *K. polycyma*; thus *K. limbata* is treated as a junior synonym of *K. polycyma*.

Holtedahl (1916) described *Strophomena brøggeri*, which Spjeldnaes (1957) referred to *Kjerulfina* (see also Bancroft 1945 : 250). In every respect *K. brøggeri* resembles *K. polycyma* except that *K. brøggeri* develops dorsal geniculates as well as ventral ones (see remarks in Spjeldnaes 1957 : 159). Obviously the species is in need of revision as it may not be a *Kjerulfina*, since no evidence of such variability has been found in the Salopian species.

Harper & Boucot (1978) suggest that *Kjerulfina* is possibly ancestral to the Strophonellidae. In support they illustrate several specimens which they assign to *K. polycyma* (Harper & Boucot 1978 : pl. 14). Two of these (pl. 14, figs 4, 12) are best assigned to *K. trigonalis*, but their locality description is inadequate to locate their stratigraphical position accurately. The remaining figured specimens are *K. polycyma* from localities used in the present study.

Figs 524–541 *Kjerulfina trigonalis* Bancroft, internal moulds of pedicle valves: 524 = lectotype BB 73834, $\times 1.5$, 525 = BB 72539a, $\times 0.9$, 527 = BB 72538, $\times 1.2$, 528 = BB 72540a, $\times 1.5$, 530 = BB 72541a, $\times 0.9$; internal moulds of brachial valves: 532 = BB 72542, $\times 1.2$, 533 = BB 73928, $\times 2$, 534 = BB 72543, $\times 1.5$, 535 = BB 73913, $\times 1.5$; external moulds of pedicle valves: 526 = BB 72539b, $\times 1.2$, 529 = BB 72540b, $\times 1.4$, 531 = BB 72541b, $\times 1.1$; external mould of brachial valve: 538 = BB 73914, $\times 1.3$. *Kjerulfina polycyma* Bancroft, internal moulds of pedicle valves: 536 = lectotype BB 9148, $\times 1.5$, 537 = BB 73895, $\times 1.3$, 539 = BB 73887, $\times 1.4$, 540 = BB 73908, $\times 1.5$, 541 = cast from BB 73908, $\times 1.5$.



524



525



526



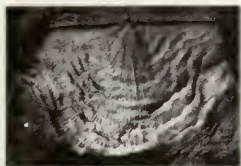
527



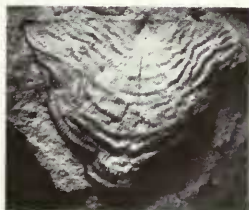
528



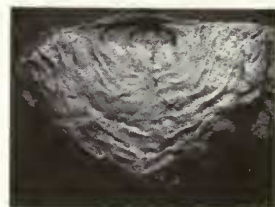
529



530



531



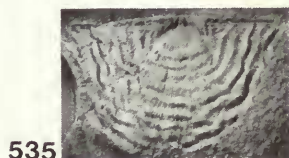
532



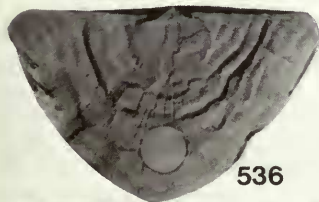
533



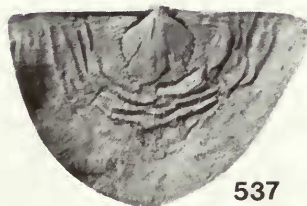
534



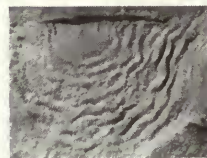
535



536



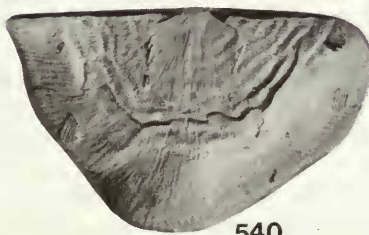
537



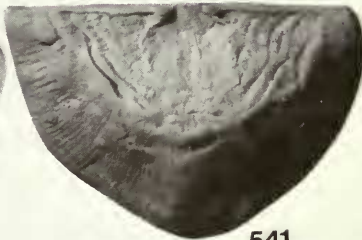
538



539



540



541

Family **CHRISTIANIIDAE** Williams, 1953Genus **CHRISTIANIA** Hall & Clarke, 1892*Christiania hollii* (Davidson)

Figs 542–557

1871 *Strophomena Hollii* Davidson : 303; pl. 42, figs 18–19.1958 '*Rafinesquina*' *holli* (Davidson) Dean : pl. 25, fig. 12.1978 *Christiania hollii* (Davidson) Cocks : 123, 200.

DESCRIPTION. Semicircular to subquadrate concavo-convex *Christiania* with pedicle valve 75% as long as wide and 30% as deep as long and occasionally with sharp-sided sulcus, nature of delthyrium unclear but with apical foramen. Ornament of raised, sharp-sided, concentric ridges.

Ventral interior with impressed oval node containing muscle field and extending forward for about 50% of the valve length, elongate oval adductor track situated posteriorly and surrounded anteriorly by diductor track, dental plates very short and divergent.

Dorsal interior with thin, widely divergent socket ridges which lie parallel to hinge line, anterior to which is anchor-shaped protegular node. Outer pair of longitudinal septa separated and displaced slightly anterior of socket ridges, inner septa short and diverging at about 40°, nature of cardinal process unknown.

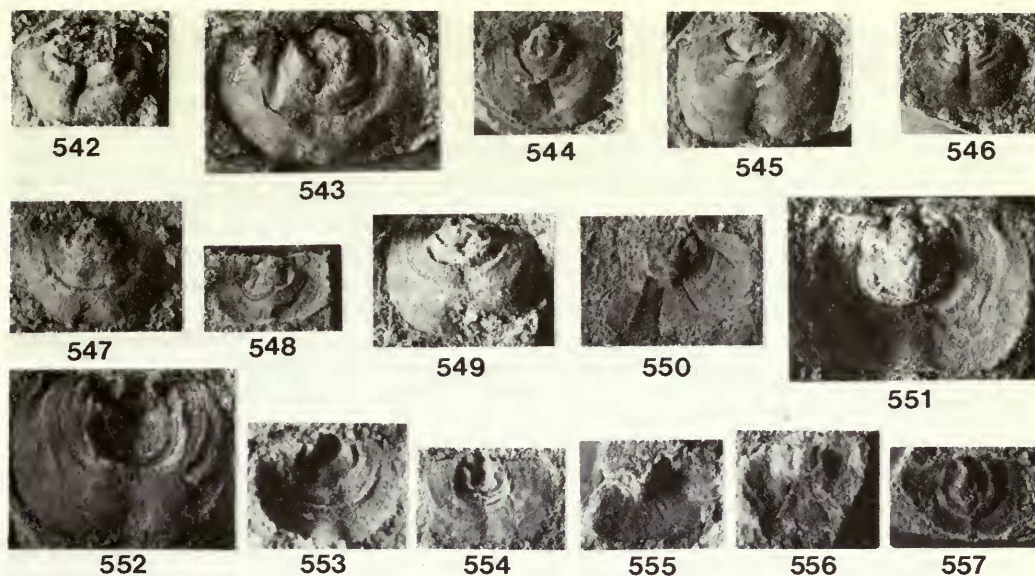
DIMENSIONS.	length	width
Internal mould of pedicle valve, BB 73610	1.4	1.8
Internal mould of pedicle valve, BB 73611	1.6	2.4
Internal mould of pedicle valve, BB 73612	1.6	2.2
Internal mould of pedicle valve, BB 73613	1.7	2.8
Internal mould of pedicle valve, BB 73614	1.9	2.6
Internal mould of brachial valve, BB 73620	1.7	2.5
External mould of brachial valve, BB 73623	1.6	2.1
External mould of brachial valve, BB 73624	1.4	2.3
External mould of pedicle valve, BB 73625	1.5	2.1

HORIZON AND LOCALITIES. Recorded from locs 50 and 51. All Davidson's type specimens are on a small block collected by Morris from loc. 51.

DISCUSSION. This peculiar brachiopod can be allocated to the genus *Christiania* on the basis of the brachial valve septa (Cocks 1978). *C. hollii* resembles the younger *C. portlocki* Mitchell from the Killey Bridge Formation of Pomeroy, Ireland (Mitchell 1977). The only obvious difference between the two species is that the young growth stages of *C. portlocki* have much finer concentric ornament. As no larger specimens of *C. hollii* exist it is difficult to compare the species any further.

Family **LEPTAENIDAE** Hall & Clarke, 1894Genus **LEPTAENA** Dalman, 1828*Leptaena salopiensis* Williams1963 *Leptaena salopiensis* Williams : 461–462; pl. 15, figs 7, 8, 10–16.

REMARKS. This species, described and figured by Williams (1963), is known from locs 35, 42–5 and 47 of the Acton Scott Formation.



Figs 542–557 *Christiania hollii* (Davidson), internal moulds of pedicle valves: 542 = BB 73612, $\times 8.4$, 543 = BB 73613, $\times 10$, 544 = BB 73616, $\times 8.3$, 545 = BB 73614, $\times 8.5$, 546 = BB 73610, $\times 9$, 547 = BB 73615, $\times 8$, 549 = BB 73611, $\times 9$; internal moulds of brachial valves: 548 = BB 73622, $\times 8.5$, 550 = BB 73619, $\times 10$, 551 = BB 73620, $\times 11.6$, 555 = BB 73618, $\times 9.5$, 557 = BB 73621, $\times 9.2$, 556 = BB 73617, $\times 9$; external moulds of brachial valves: 552 = BB 73623, $\times 13.8$, 554 = BB 73624, $\times 8.3$; external mould of pedicle valve: 553 = BB 73625, $\times 9$.

Order **SPIRIFERIDA** Waagen, 1883

Suborder **ATRYPIDINA** Moore, 1952

Superfamily **ATRYPACEA** Gill, 1871

Family **ATRYPIDAE** Gill, 1871

Subfamily **ZYGOSPIRINAE** Waagen, 1883

Genus **ZYGOSPIRA** Hall, 1862

? *Zygospira* sp.

Figs 516–521

DESCRIPTION. Small biconvex *Zygospira*, with a brachial valve 95% as long as wide and 20% as deep as long, and a pedicle valve 30% as deep as long; dorsal fold and ventral sulcus weakly developed, 35% as wide as the valve, rostrate with highly curved ventral umbo, radial ornamentation of rounded costae with up to 2 on the dorsal fold and 4 to 7 on the lateral slopes.

Ventral interior with very small teeth extending anteriorly for about 20% the length of the valve, muscle field unknown.

Dorsal interior with small, medially cleft triangular hinge plate; muscle scars not impressed.

DIMENSIONS.

	length	width
Internal mould of brachial valve, BB 72528	3.5	3.5
Internal mould of brachial valve, BB 72525	4.0	4.0
Internal mould of brachial valve, BB 72524	3.9	4.3
Internal mould of pedicle valve, BB 72523	3.3	—

HORIZON AND LOCALITIES. BB 72528 from loc. 43, colln CP4. BB 72523, BB 72526 and BB 72525 from loc. 44, collns OA10, OA13 and OA14 respectively. BB 72524 from loc. 35, colln DH1 and BB 72527 from loc. 45, colln AS3. Also recorded from locs 42 and 46.

DISCUSSION. Occasional disarticulated valves from the Acton Scott Formation are provisionally assigned to *Zygospira* on the basis of their hinge plate and valve configuration. However, the sulcal development is not reminiscent of *Zygospira*.

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